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The Nomenclature and Type Material of *Crocodylus johnstoni* (Krefft, 1873)

GLENN M. SHEA,[1,2]* CECILIE A. BEATSON[1] AND ROSS A. SADLIER[1]

[1] Australian Museum Research Institute, 1 William Street, Sydney NSW 2010, Australia

[2] Faculty of Veterinary Science, University of Sydney NSW 2006, Australia

glenn.shea@sydney.edu.au · http://orcid.org/0000-0002-0052-4205

ABSTRACT. The previously recognised original description of *Crocodilus johnsoni* Krefft, 1873 in the *Proceedings of the Zoological Society of London* is antedated by several months by a newspaper article penned by Krefft, in which the species is named as *Crocodilus johnsonii*. The same article validates the name *Tomistoma krefftii*, previously considered a *nomen nudum*. *Tomistoma krefftii* is a junior objective synonym of *Crocodilus australis* Krefft, 1867, both based on a dried head collected by William Woods near Burketown, Queensland. Both of these names potentially imperil stability of nomenclature of *Crocodylus johnstoni*, but the latter name is a *nomen protectum*, and the emendation of *johnsonii* to *johnstoni* is to be maintained due to prevailing and current usage. *Crocodilus australis* Krefft, 1867, a *nomen oblitum* with respect to *C. johnstoni*, is further a senior homonym in the genus *Crocodylus* of *Oophilus porosus* var. *australis* Gray, 1867 (another previously overlooked name), *Crocodilus australis* Bravard, in Burmeister, 1885, a Miocene fossil species from South America, currently in *Caiman*, and *Crocodylus porosus australis* Deraniyagala, 1953. The type specimen of *Crocodilus australis* Krefft is lost, but a contemporaneous archival photograph of what is presumed to be the specimen has been located. The holotype of *Crocodilus johnsonii*, originally described as just a skin, is redefined to include both the mounted skin (now missing the head) and an accompanying skeleton (now missing a skull), both bearing corresponding damage from a bullet wound at the time of collection. Archival photographs of the entire mounted skin, corresponding to a photograph sent to John Gray at the British Museum by Krefft in 1873 and to a cast of the head sent to Gray the following year, provide evidence that the head was removed from the mounted skin for casting shortly after the description of the species, and subsequently lost. A justification is provided, based on historical documentation, for the often emended type locality of *C. johnstoni* from the original Cardwell to Cashmere, Queensland.

KEYWORDS. Crocodilia; *Crocodylus johnstoni; Tomistoma krefftii; Crocodilus australis;* nomenclature; nomen oblitum; holotype

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* author for correspondence

The Australian Freshwater Crocodile, *Crocodylus johnstoni* (Krefft, 1873a), is a widespread endemic tropical Australian crocodile. The nomenclature of this iconic species has been stable since its first description, other than a dispute over whether the species name should be spelt *johnsoni*, based on the original spelling of an error in the collector's name, or *johnstoni*, a correction made by Gray (1874) at the request of Krefft, on discovering his error (see, for example, Boulenger, 1889; Wermuth, 1953; Mertens & Wermuth, 1955, Wermuth & Mertens, 1961, 1977; Cogger *et al*., 1983; King, 1989), a dispute most recently considered in detail and resolved by Tucker (2010). The species has been the subject of extensive study, some of which has been recently reviewed by Grigg & Kirschner (2015), who cite over 60 publications dealing explicitly with this species since 1975.

However, to date, there have been no detailed studies of the nomenclature and type material of this species to complement and support systematic catalogues of crocodilians and basic listings of the putative types. In this paper, we report the existence of two previously overlooked early synonyms for *Crocodilus johnstoni* and a description of this species that antedates the generally cited publication of the name, and consider the identity and status of the type material and type localities. For the purposes of this paper, we accept the arguments of Tucker (2010) and recognise the specific epithet for the species as the emended *johnstoni*, but in discussing descriptions, we use the original spelling given in each paper.

To avoid confusion, we also note here that nineteenth century authors generally used the generic name *Crocodilus* (e.g., Schneider, 1801; Gray, 1867, 1872; Boulenger, 1889; Cope, 1900), although the name is attributed to Laurenti (1768) who spelt it *Crocodylus*, and the correct original spelling of the generic name is now followed.

Krefft's description of *Crocodilus johnsoni* in the *Proceedings of the Zoological Society of London*

Krefft's (1873a) description of *Crocodilus johnsoni* in the *Proceedings of the Zoological Society of London* (hereafter referred to as *ZSL Proceedings*), which has generally been considered the original publication of the species name, bears the writing date of 31 December 1872 and a date of receipt of 17 February 1873. It was read at the meeting of the Zoological Society of 18 March, 1873, the third of six papers read at that meeting. The *ZSL Proceedings* for 1873 is printed in the form of 16 page signatures, numbered on the lower left of the first page of each signature, with Krefft's paper (appearing on pages 334–335) being part of signature number XXI, which begins on page 321 and ends on page 336. The dates of each signature are not recorded. However, Duncan (1937) notes that these pages were included in Part II (pp. 241–624), which was issued in August 1873.

Hence, the date of publication of Krefft (1873a) must be considered to be August 1873. The delay between writing and receipt of the paper reflects the time taken for mail to be shipped from Sydney to London in the era of sail. The further delay between receipt and reading, despite two other meetings of the society being held in that period (18 February and 4 March) presumably reflects the need for refereeing of the paper before formal acceptance and reading.

Krefft's paper opens by reporting that he sent a photograph of a crocodile skull to John Edward Gray, Keeper of Zoology at the British Museum, "a year or two ago", which Gray had considered to represent a new species that he proposed to call *Tomistoma krefftii*, a name which Krefft was unable to identify as being published. Krefft noted that the skull differed from the only described species of *Tomistoma*, *T. schlegelii*, in features of osteology and dentition.

Krefft then described *Crocodilus johnsoni* from "a fine and perfect skin of another Crocodile" (our emphasis) that he had received. Although it is not clear from Krefft's paper whether he regarded the earlier skull as representing the same species he described as *Crocodilus johnsoni*, it has generally been presumed that Gray's *Tomistoma krefftii* is an unpublished name introduced in the synonymy of *C. johnsoni* (e.g., Wermuth, 1953; Mertens & Wermuth, 1955; Wermuth & Mertens, 1961, 1977; Cogger *et al*., 1983) and hence unavailable for nomenclatural purposes. This argument is supported by the inclusion with Krefft's paper in the *ZSL Proceedings* of a letter from Gray, in which he suggests that the earlier photograph of a head is likely to be the same species for which he had proposed the name *Tomistoma krefftii*. However, as Krefft presumably had not seen Gray's letter at the time of writing his paper (Gray notes that he had been sent a photograph of the whole skin, with the request to communicate to the Society some comments on it), Krefft's extensive initial commentary on *Tomistoma krefftii* and his statement that the holotype of *Crocodilus johnsoni* was "another Crocodile" could be interpreted as the two names being applied to different species in Krefft's mind.

That this interpretation is correct is apparent from an article Krefft wrote for the Sydney newspaper, the *Sydney Mail and New South Wales Advertiser* (hereafter referred to as the *Sydney Mail*), published as part of a series by Krefft under the initial banner "The Natural History of New South Wales". This series was begun by Krefft in the issue of 4 March 1871, with the stated purpose of trying to counter a deficiency in the availability of works on the Australian fauna "by giving in the columns of the Sydney Mail a series of articles on our natural history, which, in course of time, will form a complete work on the subject" (Krefft, 1871), and continued until 23 January 1876, although the initial standard title for the series was dropped in favour of more specific titles reflecting the group of organisms being described in each article.

On 4 January 1873, just four days after writing his manuscript sent to the Zoological Society, over a month before that manuscript was received by the Society, two months before the manuscript was read by the Society, and eight months before it was published, an article by Krefft on Australian crocodiles appeared in his series in the *Sydney Mail*.

Krefft's description of Australian crocodiles in the *Sydney Mail*

Krefft's (1873b) article in the *Sydney Mail*, titled "Remarks on Australian Crocodiles", lists the species of crocodiles recorded from Australia, and provides a description of each. He lists four species:

1 *Crocodilus porosus*
2 *Tomistoma Schlegelii*
3 *Tomistoma (?) Krefftii*
4 *Crocodilus Johnsonii*

Each species is accompanied by a short diagnostic description. That Krefft at the time considered *Tomistoma krefftii* distinct from *Crocodilus johnsonii* is also apparent from his first statement under the latter species: "there must be at least three long-snouted crocodiles in northern Queensland, if the number of teeth is of consequence in classification." (These being *Tomistoma schlegelii*, *T. krefftii* and *C. johnsonii*—the record of *T. schlegelii* in Australia is presumably from the distribution statement "Australasia, Borneo" for that species by Gray, 1867, 1872, although this is not explicitly stated by Krefft).

This article has two consequences for nomenclature. Firstly, it antedates the generally recognised description of *C. johnsoni* by several months, and hence must be regarded nomenclaturally as the first description of the species. This has little nomenclatural effect, as the description of the species by Krefft in the *Sydney Mail* (1873b) largely parallels the description by Krefft in the *ZSL Proceedings* (1873a) in terms of the characters mentioned, although the exact words used differ in several places, and the type specimen is the same. That Krefft (1873b) uses *C. johnsonii* in the newspaper article and uses *C. johnsoni* in the *ZSL Proceedings* (1873a) is of little consequence—under the Code the two names are homonymous (Article 58.14 of the International Code of Zoological Nomenclature), although the *-ii* termination has priority, based on the discovery of the earlier description by Krefft (1873b).

The second consequence is that *Tomistoma krefftii* is validated as an available name in this paper, distinct from *C. johnsoni*. Krefft's account clearly states that *T. krefftii* differs from *T. schlegeli* in possessing 19–20 teeth in the upper dental arch and 15 in the lower dental arch (*vs* 20 and 18 respectively for *T. schlegeli*) and has the mandibular symphysis extending only to the sixth tooth (*vs* the fifteenth tooth for *T. schlegeli*). His use of a question mark in the generic assignment is explained by his commentary on the extent of the mandibular symphysis, where *Tomistoma* was diagnosed in the literature by the great extent of the symphysis ("not having the necessary literature at my disposal, I cannot decide whether this crocodile should be made into a new genus or not" he wrote).

Krefft noted that *Tomistoma krefftii* is "founded upon a skull which I received from a gentleman of northern Queensland. It was stated that the animal grew to a length of about five or six feet, and frequented the lagoons of the interior. Dr. J. E. Gray, of the British Museum, described it from a photograph sent to him". With Gray never having published his description of *T. krefftii*, the formal description of the species, and validation of the name with at least one purported diagnostic character not available to Gray, must be the description provided by Krefft (1873b), although Krefft attributed the name to Gray in that article. Hence, we refer to the validated publication of the name *Tomistoma krefftii* as by Gray as given in the newspaper article in the *Sydney Mail* by Krefft (1873b).

Who was the unnamed "gentleman of northern Queensland"? Further study of Australian newspaper archives, now readily available through the Australian Newspaper Digitisation Program, has uncovered an earlier article by Krefft (1867) that resolves this issue, but adds yet another nomenclatural twist.

Krefft's 1867 article in *The Australasian*

The 1867 article by Krefft, published in a Victorian newspaper on 27 July 1867, begins with a discussion of the application of the name alligator and crocodile with respect to *Crocodilus porosus*, which had often been referred to colloquially, but incorrectly, as an alligator. It then states:

> "Besides this large species, the range of which extends as far as India, we have another smaller kind, for which I have proposed the name of *Crocodilus Australis*. This little crocodile has a much more slender snout, almost as slender as a gavial, and the production outwards at the end is scarcely perceptible; the bones of the head are less rugose, and the teeth not so conical as those of *C. porosus*; there are nineteen in the upper jaw and fifteen in the lower. *C. porosus* has eighteen and fifteen respectively.
>
> "I am indebted to Mr. William Wood, who has lately returned from the Gulf of Carpentaria, for a skull of this new crocodile, which is ten inches in length, the whole animal being about four or five feet. Mr. Wood informs me that these reptiles are plentiful in all the lagoons and waterholes in the neighbourhood of the gulf, and that they never grow larger than about seven or eight feet in length."

The head/skull referred to by Krefft in 1867 is presumably the same as that of which a photograph was sent by Krefft to Gray "a year or two" before the description of *C. johnsoni* in 1873, and on which Gray based his manuscript name *T. krefftii*, but the article also creates and nomenclaturally validates another name for *C. johnstoni*—*Crocodilus Australis*—which antedates all others. It would appear that Krefft forgot that he had named the species *C. australis* when he sent the photograph to Gray a few years later.

What is the evidence that the skull Krefft described as *Crocodilus australis* in 1867 is the same specimen that Gray was sent a photograph of in 1871, and that served as the basis for the *Sydney Mail* description (Krefft, 1873b) of *Tomistoma krefftii*? Krefft (1867) noted that William Wood, from whom he had obtained the skull, had "lately returned from the Gulf of Carpentaria". Hence, Krefft had only recently received that specimen by July 1867, when his description of *Crocodilus Australis* appeared. The skull/head for *Tomistoma krefftii* must have been received by the end of 1871. Hence, the 1867 acquisition date of the skull of *Crocodilus Australis* would be concordant with the time lapsed when Krefft (1873a) noted that he had sent a photograph of it to Gray "a year or two ago", and with the comment by Gray (1874) that Krefft had sent to him the photograph of the skull on which the manuscript name was based in 1871.

There is no evidence for any other Freshwater Crocodile being obtained by the Australian Museum between 1867 and 1871. Monthly lists of donations of specimens to the Australian Museum were published in the local press, particularly in the *Sydney Morning Herald*, during Krefft's tenure at the Australian Museum. Annual listings of donated specimens were also included in the Museum's Annual Reports. While the monthly lists published in the Sydney press are not complete for all months between 1867 and 1871, there is a reasonably complete record, complemented by the annual listings. The first record of donation of any crocodiles to the Museum post 1867 is the receipt of two specimens in March 1872, both identified as *Crocodilus porosus*: one donated by the owners of the schooner *Spunkie*, received from Captain Brown; the other a young individual donated by Thomas Spence (Krefft, 1872). The receipt of these specimens was so unusual that it prompted a note appended to the list for that month by Krefft (as "G.K.") commenting again on the difference between alligators and crocodiles, and noting that Gray had already 'described a "false gavial" from Australia as *Tomistoma Krefftii*.' Regardless, this use of the name *Tomistoma Krefftii* is a *nomen nudum*, but does further indicate that Gray had been sent the photograph of the head by Krefft, and that Krefft had received return correspondence on this proposed identification, by March 1872. That Krefft could no longer remember the name of the donor of the skull of *Tomistoma krefftii* by 1873, merely referring to "a gentleman of northern Queensland", also implies a date of collection closer to 1867 than 1873.

The existence of the name *Crocodilus australis* Krefft, 1867 potentially threatens the stability of nomenclature of the Australian Freshwater Crocodile, and further, it is a potential homonym of three other taxa.

The other three *australis* epithets among crocodiles

Augusto Bravard, an Argentine-based French paleontologist, compiled a monograph of the fossil fauna of the marine terraces of Parana, published among the official papers of the Argentine National Government in 1858, in which he erected the taxon *Crocodilus australis* for all non-longirostrine crocodiles in those deposits. The name was published again by Bravard (1860) in a catalogue of his collections privately printed in Paris (Langston, 1965; Bona *et al*., 2013). Bravard died in the March 1861 earthquake in Mendoza, Argentina (Burmeister, 1885).

Both publications are rare, and we have not been able to trace original copies of them. However, German Burmeister reprinted Bravard's (1858) monograph in 1883, and we have used this version as representing the 1858 original publication.

Crocodilus australis in this sense was transferred to a new genus *Proalligator* by Ambrosetti (1887), to *Alligator* by Rovereto (1912), to *Jacaretinga* by de Saez (1928), to *Caiman* by Kälin (1936), back to *Proalligator* by Langston (1965) and most recently has returned to *Caiman*, where it is recognised as a distinct species (Bona *et al*., 2013).

Patterson (1936) and Langston (1965) considered *Crocodilus australis* Bravard (1858) to be a *nomen nudum*, due to the description being insufficiently detailed to distinguish the species, and attributed the name to Burmeister (1885), who provided a more extended description and diagnosis while still attributing the name to Bravard. Bravard's (1858) description states "Dientes bien conservados, fragmentos del cráneo, de las placas dorsales de la coraza y una vertebra perfecta. De las placas duda mucha si son en verdad del cocodrilo; pueden ser tambien de pescados", or, loosely translated: "Well preserved teeth, fragments of skull, dorsal armor plates and a perfect vertebra. Of the plates, there is much doubt if they are really crocodile; they could also be fish". It is clear that this is merely a statement of the material collected, without diagnostic characters sufficient to validate the name nomenclaturally (Article 12.3 of the Code of Zoological Nomenclature). Hence, the name *Crocodilus australis* as applied to the South American species must be attributed to Bravard in Burmeister (1885), making it a junior primary homonym of *Crocodilus australis* Krefft rather than the senior primary homonym that would be the case if Bravard had provided any diagnostic or descriptive details prior to his death.

The second use of *australis* with crocodiles is by Deraniyagala (1953) who, while describing Sri Lankan populations of the Saltwater Crocodile *Crocodylus porosus*, noted "The Australian form with its clusters of numerous raised post-occipital scutes might be termed *Crocodylus porosus australis* ssp. nov. (*Vide* Barrett 1950. *Reptiles of Australia* Cassell & Co., p. 12)." As noted by Mertens (1960), the plate in Barrett (1950) facing p. 12, while labelled as a Saltwater Crocodile, is of an American Alligator, *Alligator mississippiensis*, and clearly shows numerous raised post-occipital scutes, while there is no mention of this character, or of any other species-specific morphological character, on p. 12, and it is assumed that Deraniyagala's citation of p. 12 is a reference to the unnumbered plate facing this page. That Deraniyagala cited the incorrect page number does not invalidate the name nomenclaturally, as he stated the purported diagnostic character in his publication rather than merely making the name available by bibliographic reference to a diagnostic statement. Deraniyagala's name *Crocodylus porosus australis* has been placed in the synonymy of *Alligator mississippiensis* by Mertens (1960), and Wermuth & Mertens (1961), and it is hence unavailable for the Australian populations of *Crocodylus porosus* (although Wermuth & Mertens, 1977 and Cogger *et al*., 1983 retain it in the synonymy of *Crocodylus porosus*).

The third use of the name *australis* in crocodiles does, however, unequivocally relate to Australian populations of *Crocodilus porosus* and, like *C. australis* Krefft, appears to have been overlooked by all subsequent researchers. Gray (1867), while describing the Saltwater Crocodile (under the combination *Oophilus porosus*), noted that Australian populations differed from Indian populations in having "one cross band of the shield less than the Indian specimens; that is to say, they have sixteen, and the Indian specimens seventeen bands of shields from the neck to the base of the tail." Consequently, he used the name "var. *australis*" for Australian populations, though attributing the name to Alfred Günther, who had pointed out the difference to him. This stated diagnostic character is sufficient to validate the name *Oophilus porosus* var. *australis* for Australian populations of *Crocodilus porosus*, and antedates Deraniyagala's *Crocodylus*

Figure 1. Left lateral view of a dried head of *Crocodylus johnstoni*, possibly the holotype of *Crocodilus australis* Krefft and *Tomistoma krefftii* Gray, in Krefft (image created from Negative V343, Australian Museum Archives).

porosus australis by 86 years. The use of varietal status for the taxon qualifies as subspecific recognition (Article 45.6.4 of the Code of Zoological Nomenclature). Gray (1872) repeated the diagnostic statement. Both Gray (1867) and Krefft (1867) were published in the same year. Relative priority can be determined from the literature. Krefft's description, published on 27 July, antedates Gray's description, which was published on 5 November (Peavot, 1913).

Hence, in summary, *Crocodilus australis* Krefft, 1867 is a senior primary homonym of *Crocodilus australis* Bravard in Burmeister, 1885 (now *Caiman australis*), a senior secondary homonym in *Crocodylus* of *Oophilus porosus* var. *australis* Günther in Gray, 1867, but, by one letter difference in the generic name, not a homonym (but see Article 57.5 of the Code of Zoological Nomenclature for an alternative view, if *Crocodilus* is considered an incorrect subsequent spelling of Laurenti's *Crocodylus*) of *Crocodylus porosus australis* Deraniyagala, 1953, a synonym of *Alligator mississippiensis*, although intended by that author as a name for Australian populations of *Crocodylus porosus*, where it would have been a junior secondary homonym of Krefft's name as well as that of Günther in Gray (and a junior synonym of the latter). Whether Australian populations of saltwater crocodiles warrant subspecific recognition remains largely unstudied.

The type material of *Crocodilus australis* Krefft, 1867 and *Tomistoma krefftii* Gray, in Krefft, 1873

Krefft (1867), when describing *Crocodilus Australis*, refers to the specimen as a skull. However, the form of the same specimen when described as *T. krefftii*, is variably stated as either a skull or a head. Krefft (1873a) first states that he sent Gray a photograph of the skull, and notes that the skull was damaged during preparation (it is unclear whether this was Krefft's preparation of the skull, or prior preparation by the donor). On the same page, Gray's accompanying letter refers to the photograph sent to him as being of the "upper part of the head". On the next page, Krefft further states that the character state of the mandibular symphysis was apparent to him "only since the skin had been removed from the skull", suggesting that it was Krefft who removed the skin and prepared the skull, after sending a photograph of the head to Gray. However, it is possible that Krefft was actually saying that only he was able to examine the mandibular symphysis, since only he had the opportunity to examine the ventral surface of the skull, as Gray had been sent only a dorsal photograph.

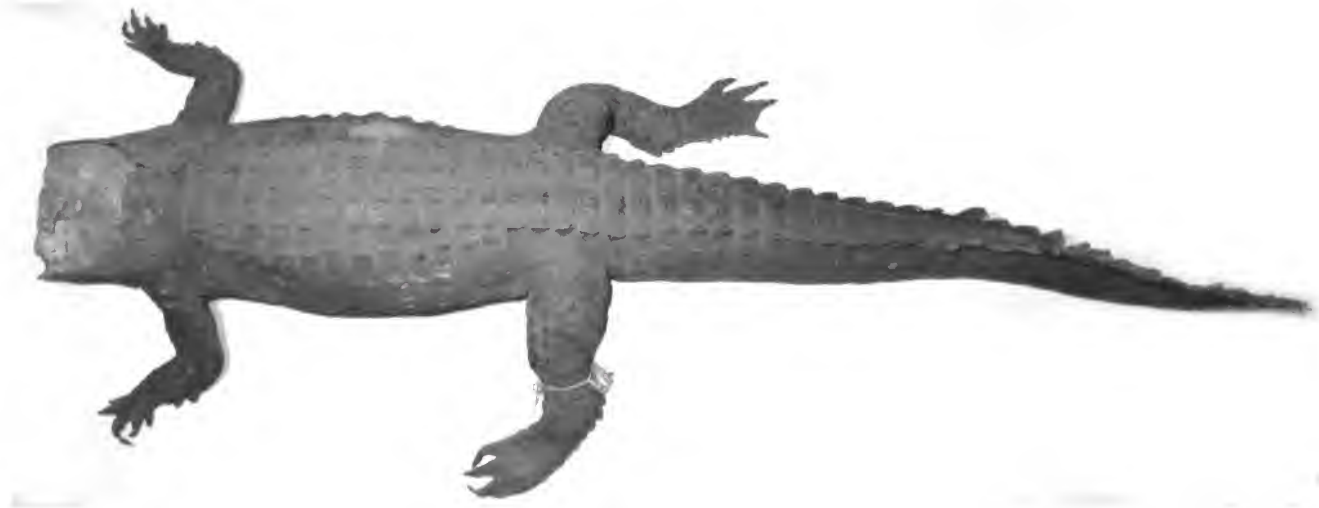

Figure 2. Dorsal view of holotype skin of *Crocodilus johnsonii* Krefft.

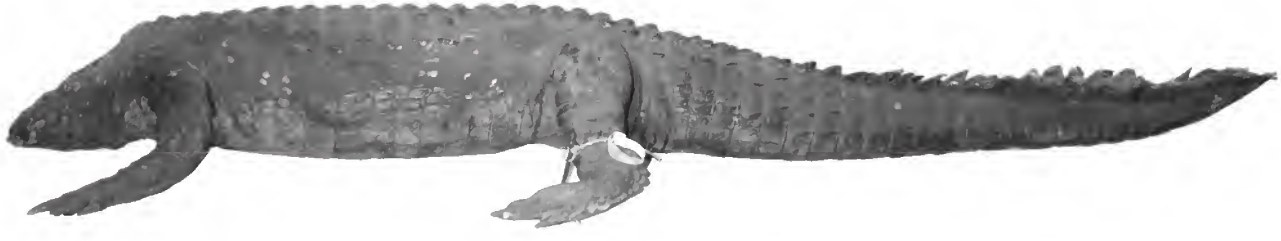

Figure 3. Left lateral view of holotype skin of *Crocodilus johnsonii* Krefft.

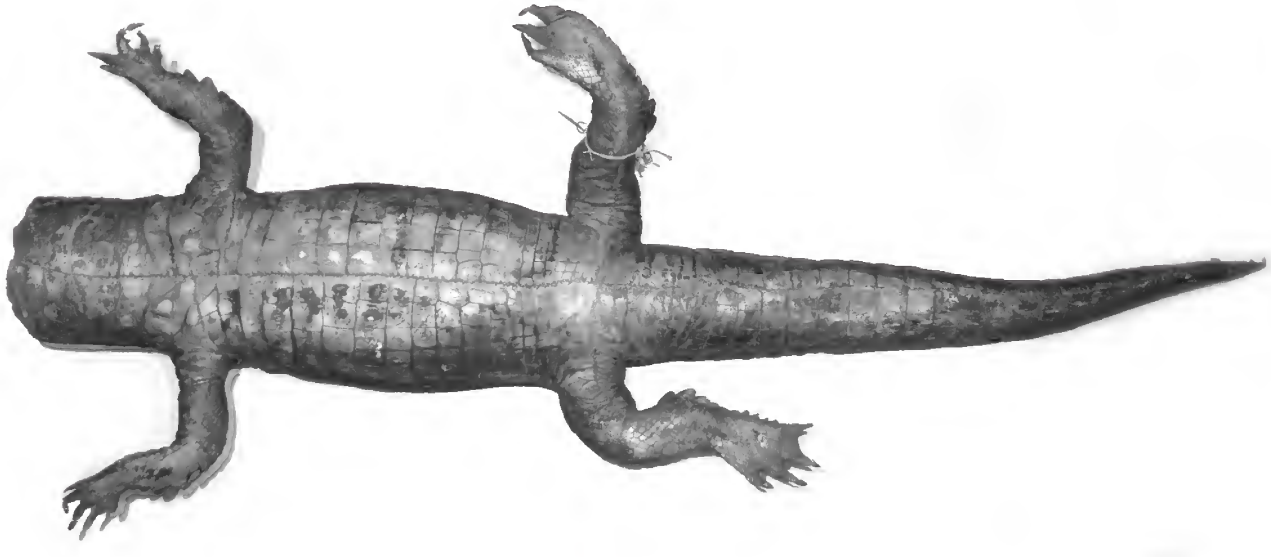

Figure 4. Ventral view of holotype skin of *Crocodilus johnsonii* Krefft. Note the low number of transverse ventral scale rows on the body, diagnostic of this species.

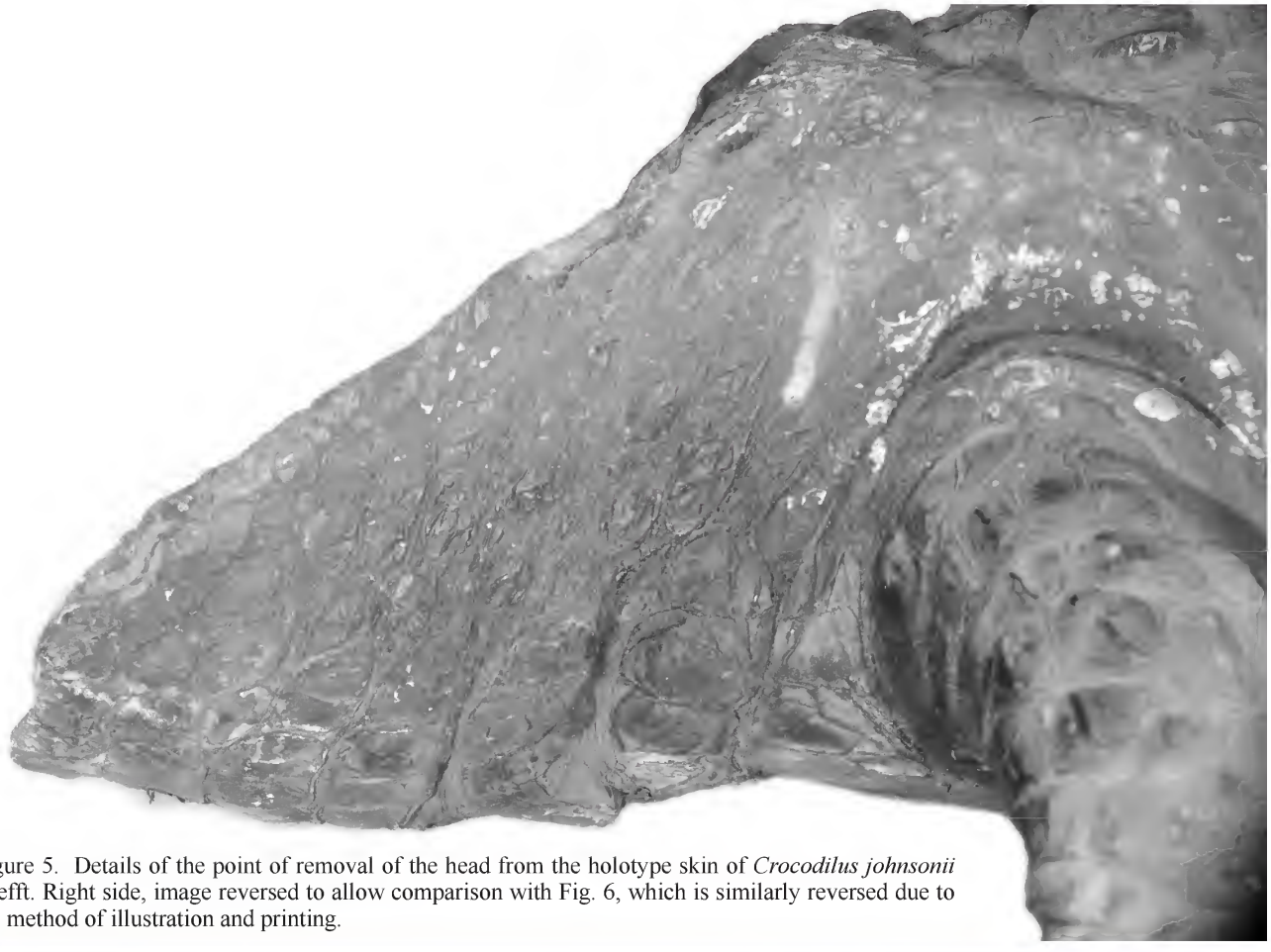

Figure 5. Details of the point of removal of the head from the holotype skin of *Crocodilus johnsonii* Krefft. Right side, image reversed to allow comparison with Fig. 6, which is similarly reversed due to the method of illustration and printing.

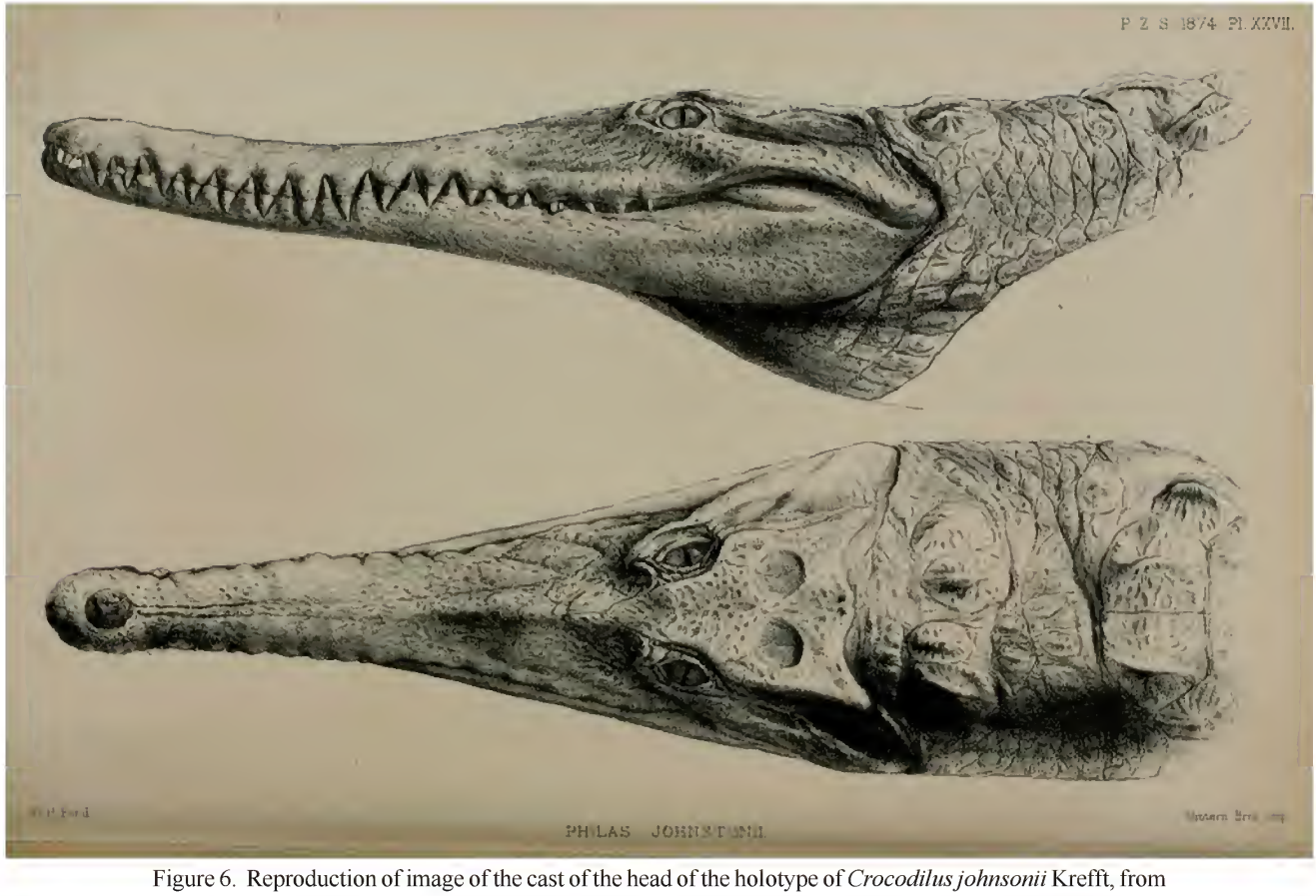

Figure 6. Reproduction of image of the cast of the head of the holotype of *Crocodilus johnsonii* Krefft, from Gray (1874). Note correspondence of the posterior edge of the cast with the anterior edge of the holotype skin.

The combination of Krefft's (1873a) description of the damage to the specimen (damage by rats, with a broken rostrum and several missing teeth), and his earlier description of the skull being ten inches long, from an individual four or five feet long, should facilitate identification of this specimen among the skulls of *Crocodylus johnstoni* in the Australian Museum collection, if still present.

However, our search of the crocodile skulls among the early collections, and examination of registration records (the earliest Australian Museum collection registers postdate Krefft's era) has not revealed any suitable candidate specimen of the size and damage described, and we consider the skull that represents the holotype of both *Crocodilus australis* and *Tomistoma krefftii* to be lost. Indeed, there is no mention of this specimen in the monthly and annual Australian Museum donation lists for 1867, raising the possibility that it may have been retained by the collector after having been shown to Krefft and photographed by him.

The photograph of the type of *Tomistoma krefftii* sent by Krefft to Gray can now no longer be located in the Natural History Museum, London (P. Campbell, pers. comm.). While there is much Krefft correspondence in the Natural History Museum Archives, which the senior author has examined, no photographs are associated with the letters, and the crocodile correspondence cannot be located.

However, the Australian Museum Archives holds a glass plate negative (V343 in the Register of Negatives) of a lateral view of the dried head of a *Crocodylus johnstoni* (Fig. 1), depicted lying on a wooden bench with a 2 inch scale bar attached to the edge of the bench. Based on this scale bar, the head is approximately 10 inches long, and several teeth at the anterior end of the rostrum are missing. The Register of Negatives postdates Krefft's era, and the negatives are arranged in taxonomic order (reptile images are entered in the series V340–V361), and hence there is no useful information to be gathered from the order of registration on the date each negative was created. The negatives in the series are identified in the register as having been created by H. Barnes, presumably Henry Barnes Senior, who was taxidermist/photographer during Krefft's curatorship, ending in 1874. Henry Barnes (4.iv.1838–17.iii.1898) was employed by the museum between 1859 and 1897; his son, Henry Edward Barnes (Henry Barnes Junior), was employed by the museum between 1878 and 1913 (Strahan, 1979). This cannot be the negative for the photograph sent to Gray by Krefft, as it shows a lateral view rather than a dorsal view, but it may be one of a series taken at the same time. If this photograph does represent the holotype of *Crocodilus australis* and the specimen of which the photograph was sent by Krefft to Gray on which the name *Tomistoma krefftii* was based, it must have been taken before the skin was removed and the rostrum damaged (broken and chewed by rats), as no such damage is apparent (at least on the left side of the head).

In the absence of extant type material, it becomes important to attempt to match any archival material available of the type specimen to a particular location or population from which the type was sourced, to stabilize the taxonomy and nomenclature of the species.

Where did William Wood collect in northern Queensland?

That Wood gave the specimen to Krefft shortly before Krefft described it as *Crocodilus australis* in July 1867 provides sufficient information to track Wood's source population. By July 1867, the only settled port in the Gulf of Carpentaria was Burke Town (also known in contemporary records as the Albert River Settlement, and now known as Burketown), which was established in 1865. The other coastal towns, Normanton and Karumba (initially known as Kimberley), were not established until 1867 in the case of the former and the 1870s for the latter. Examination of the published shipping records reveals the departure of a Mr W. Wood from Burke Town as one of two passengers (the other the local Police Lieutenant Wentworth D'Arcy Uhr, who was accompanying a prisoner) departing from Burketown aboard the schooner *Salamander* on 17 April 1867, and arriving in Sydney on 9 July, after a rough passage around the west coast of Australia and through Bass Strait (Anonymous, 1867a–c).

Hence, William Wood arrived in Sydney 18 days before the publication of the description of *Crocodilus australis*, and had been based in Burketown, which must be considered an approximate locality for the collection of the type. It is not clear how long Wood had lived in Burketown—we have been unable to find any record of his arrival in shipping records. He may have come to the district overland from Port Denison (now Bowen), along with many of the early settlers.

The type material of *Crocodilus johnsonii* Krefft, 1873

That Krefft (1873b) did not regard *Tomistoma krefftii* as conspecific with *C. johnsonii* at the time of description of the latter, clearly implies that the type of *T. krefftii* cannot be considered a part of the type series of *C. johnsonii*, although this is not obvious from the second description of the latter species (Krefft, 1873a) in the *ZSL Proceedings*.

Hence, the description of *Crocodilus johnsonii* by Krefft (1873b) must be based solely on the specimen collected by Mr Johnson [sic]. Krefft specifically states in both of his papers of that year that the specimen was the skin of a crocodile 7 feet in length, with the head 1 foot 4 inches. He further notes details of the head and neck in the description, which together with the total length given, indicates that the head was part of the skin at the time of the description.

Subsequently, the holotype of *Crocodilus johnsonii* has been considered to be represented by two specimens in the Australian Museum collection: a stuffed skin missing the head, registered in the Palmer Register as 4627, but now reregistered in the herpetology collection as AM R134547 (Figs 2–4), and an articulated skeleton, initially 4629 in the Palmer Register, but now AM R134548, considered to be from the same animal (Cogger, 1979; Cogger *et al*., 1983; King, 1989; Shea & Sadlier, 1999). The Palmer Register has annotations for these two entries that appear to be in the hand of Allan McCulloch, employed by the Museum between

1901–1925. These state that the head was cast, and that the skeleton represented the same individual as the skin. This information is noted as being obtained from Edward Pierson Ramsay, who succeeded Krefft and died in 1916. Hence, these annotations are likely to have been made between 1901 and 1916, at least 27 years after Krefft's departure from the Museum, and at least 20 years after Krefft's death.

There is no record of when the head was removed from the rest of the skin, but the incisions on the remaining stuffed skin are certainly not fresh (Fig. 5). Gray had been sent a photograph approximately 22 inches long, showing a dorsal view of the whole specimen of the holotype of *C. johnsonii* (Gray, in Krefft, 1873a), while one year later Gray (1874) illustrated the head of the species, based on a plaster cast of the head of the holotype sent to him by Krefft.

The posterior margins of the illustration of the head (Fig. 6) provided by Gray (1874) correspond closely to the margins left on the remaining portion of the mount, and hence we presume that the head was removed by Krefft in 1873, shortly after the description of the species, to prepare the mould for the plaster cast and subsequently prepare the skull. The shape of the plaster cast illustration in Gray's (1874) paper indicates that the intact skull was still inside the head when it was cast. Preparation of the skull would have involved destruction of the skin of the head, which is firmly attached to the skull in crocodilians. The mould created for casting by Krefft could also provide a replacement head cast to complete the mounted skin for display following skull extraction, although this does not seem to have been done (possibly overlooked in the tumult following Krefft's dismissal as Curator in 1874—Pigott & Strahan, 1979). The mounted skin bears no evidence of glue or paint at the cut margins, although there is a little residual plaster along the ventral suture line, and there are no entries in the Australian Museum Register of Casts (the L Register) or Register of Moulds (the T Register) of a cast or mould of the whole head of either Palmer Register 4627 or 4629. The Register of Moulds, however, does include an entry relating to the mandible of Palmer Register 4629 (the skeleton), a mould registered as T71 (entered in September 1904, but copied from an older entry), and the Register of Casts has two entries for the mandible of Palmer Register 4629. The first, L71, bears no annotation that it was taken from the holotype mandible, but does bear a reference to the number 69, a number that also appears in association with the Mould Register entry for T71, but which we have not otherwise been able to trace. The second entry, L1462, registered on 27 July 1921, is specifically linked in the original entry to mould T71. This cast was recorded at the time of entry as part of the "Old Collection". It is not clear whether L71 from 1893 and L1462 from 1921 are the same cast, but neither has been further traced in the Australian Museum collection.

As the head and most of the dorsum of the neck are now missing from the mounted skin, precluding examination of many of the purported diagnostic features of the species relating to dentition, head shape and arrangement of nuchal plates, and as the purported holotype skin was not registered until several years after the description (the Palmer Register, the first register mentioning the specimen, was compiled between 1877 and 1880, and number 669, assigned to a mammal specimen, which appears well before the number assigned to the crocodile skin, has been interpreted as being assigned about 1879—Parnaby *et al.*, 2015), it is important to ensure that the skin actually does represent the holotype, and the species currently assigned the name *C. johnstoni*, rather than being a later substitute.

The major character states described from body, tail and limbs (the components still present on the skin) by Krefft (1873a,b) relate to the dorsal shields. Krefft describes those of the body as being one single row, one of two scales, two rows of four, two rows of six, seven rows of eight (the outer ones feebly keeled), two rows of six, and four rows of four, giving 19 rows to the base of the tail, with the tail in turn encircled by 29 bands of scales. All of these features are present on the extant portion of the mount. Given the correspondence of the cast of the head in the then British Museum collection (Gray, 1874; Boulenger, 1889) with the remaining mount in the Australian Museum, we consider that the remaining portion of the stuffed skin is assignable to the holotype specimen. While this specimen now lacks the cranial and nuchal features diagnostic of *Crocodylus johnstoni* (e.g., Cogger, 2014), it is identifiable as that species on the basis of the presence of osteoderms in the ventral body scales, and approximately 24 transverse rows of ventral body scales from the posterior nuchal collar to the anterior margin of the vent (Brazaitis, 1987).

The mounted skin is now black, possibly due to painting. There is some flaking of what appears to be thin paint on some dorsal scales. Consequently, the original pattern described by Krefft is no longer apparent.

The cast of the head of the holotype of *C. johnstoni* in the Natural History Museum, London, although mentioned as being present by Boulenger (1889) and King (1989) (the latter author may have simply based his statement on that of Boulenger), is no longer able to be located in the collection, and the herpetology catalogue lists it as unregistered (P. Campbell, pers. comm.). Hence, the only information that can be obtained from it is from the illustration of the cast provided by Gray (1874).

However, there are glass plate negatives in the Australian Museum Archives (V340–342, V344–345) that appear to represent the holotype stuffed skin. The first three of these negatives, which, like the other negatives in the series, are on standard 8×6 inch glass plates (c. 202×152 mm), represent a sequence of three segments of the specimen: head, torso and tail, with overlap between the images (Figs 7–9). Abutting these plates and exposing them directly onto photographic paper would have created an image about 22 inches long, assuming either some trimming of the blank space in front of the tip of snout and tip of tail, or overlapping of the plates in sequential exposures to eliminate redundancies (each image has what appears to be chalk marks between transverse rows of scutes on neck and tail that allow alignment of the images, although there are some perspective changes between images that prevent perfect alignment). V344 (Fig. 10) is a lateral view of the whole mount, placed on a timber table (but not the same table as the image of the possible type of *C. australis*), and V345 (Fig. 11) is a dorsal view of the whole animal, seemingly placed against the same white drape apparent on the wall in Fig. 10. All five negatives, which are identified in the Register of Negatives as *Philas johnstonii* (or possibly *johnstonei*—the handwriting could be interpreted either way), are clearly of the same specimen, and the torso and tail of the specimen correspond to the extant portions of

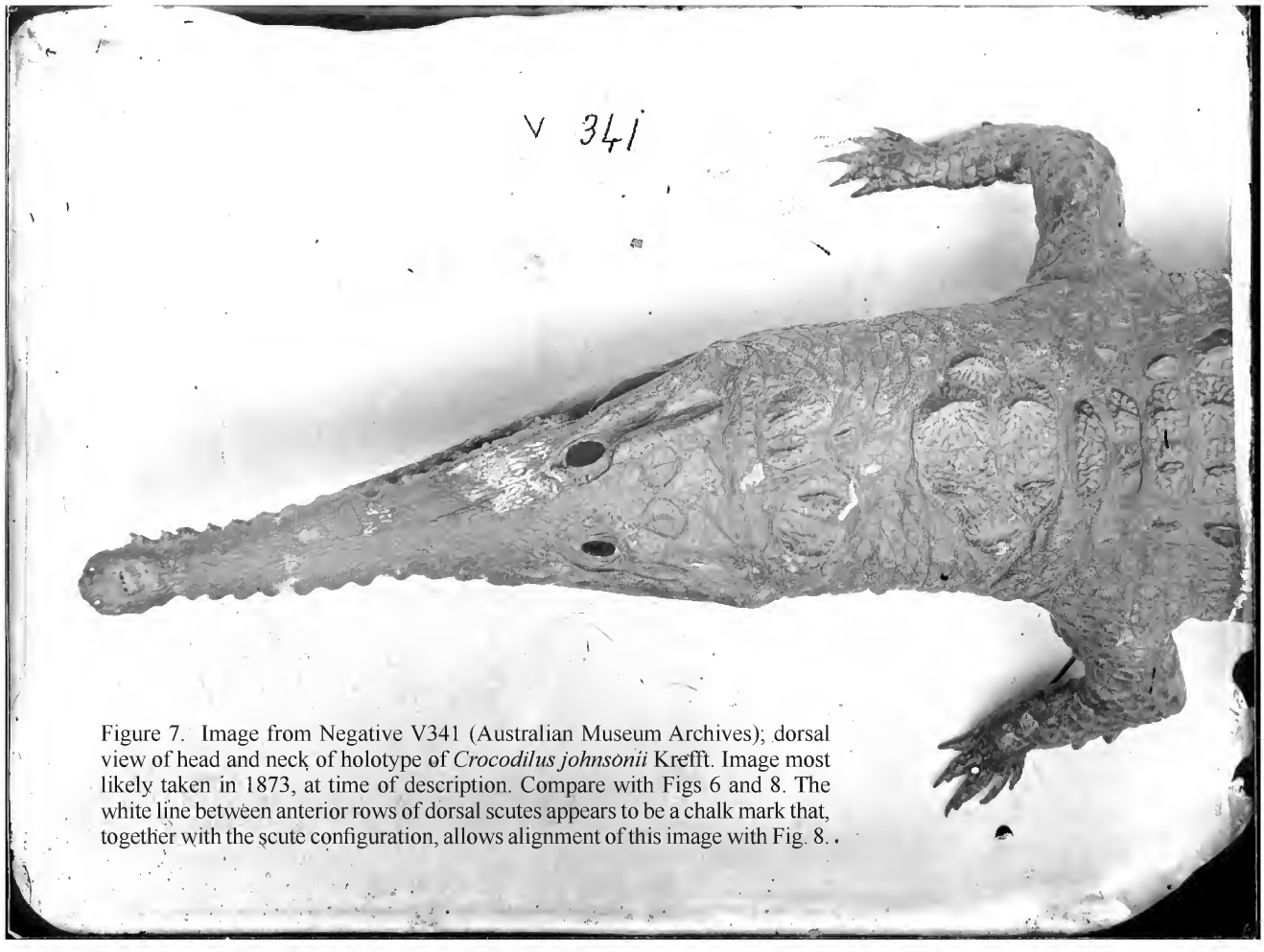

Figure 7. Image from Negative V341 (Australian Museum Archives); dorsal view of head and neck of holotype of *Crocodilus johnsonii* Krefft. Image most likely taken in 1873, at time of description. Compare with Figs 6 and 8. The white line between anterior rows of dorsal scutes appears to be a chalk mark that, together with the scute configuration, allows alignment of this image with Fig. 8.

the holotype skin. The specimen represented is different to the head in image V343 (which we consider to represent the type of *Crocodilus australis* and *Tomistoma krefftii*).

These images, all identified as being taken by H. Barnes, would seem to be the basis of the 22 inch photograph sent to Gray in 1873, and would seem to represent the specimen prior to removal of the head for casting. However, there is one major discrepancy between the photographs and the cast. V344 shows the mouth of the mounted skin to be open, while the cast has a closed mouth. It is possible that Krefft forced the mouth closed prior to casting, to simplify the casting process. The position of the articulation between mandible and quadrate relative to the postarticular skin impression on the cast would have resulted in any tissue compression caused by closing of the mouth lying within the mouth (and hence not visible on the cast), while the relatively small amount of postarticular skin would be slightly stretched. Further, from comparison of the photograph of the head in dorsal view (Fig. 7) with Gray's 1874 figure (Fig. 6), it is apparent that Gray's figure is reversed, as might be expected from a print made from a lithographic etching that was not initially drawn in reverse (Gould, 1996; the reversal is most obvious in the asymmetry of the nuchal shields, but also apparent in more subtle asymmetries).

Krefft (1873a,b) makes no mention of a skeleton. The articulated skeleton that has subsequently been considered part of the type (Fig. 12) is currently missing the skull, although this has evidently been removed from the mount at some time after preparation, as the steel rod passing through the vertebral canal to articulate the vertebral column extends 11 cm beyond the atlas to form a support for a skull.

There is currently only one isolated skull of *Crocodylus johnstoni* in the Australian Museum collection that lacks locality and collector data (R179146). From comparison of this skull with the illustration of the cast of the head of the holotype presented by Gray (1874), viewed in reverse, together with the observation by Krefft (1873a,b) that the head of the holotype was 1 foot 4 inches long (= 406 mm, although the reference points for this measurement were not provided), R179146 can be excluded from consideration as the missing holotype skull, as it has a midline skull length of 370 mm, a lateral skull length of 390 mm, and mandibular teeth 12–13 both interposed between teeth 12–13 of the upper dental arch.

Another possibility for the missing skull is that it is represented by the photograph provided by Waite (1929: 56) in his *Handbook of the Reptiles and Amphibians of South Australia*. Edgar Ravenswood Waite (5.v.1866–19.i.1928), prior to his appointment as curator of the South Australian Museum, was employed at the Australian Museum between 1893–1906, and hence would have had the opportunity to obtain photographs of the holotype. No *Crocodylus johnstoni* skull corresponding to this photograph can be located in the South Australian Museum collection (C. Kovach, pers.

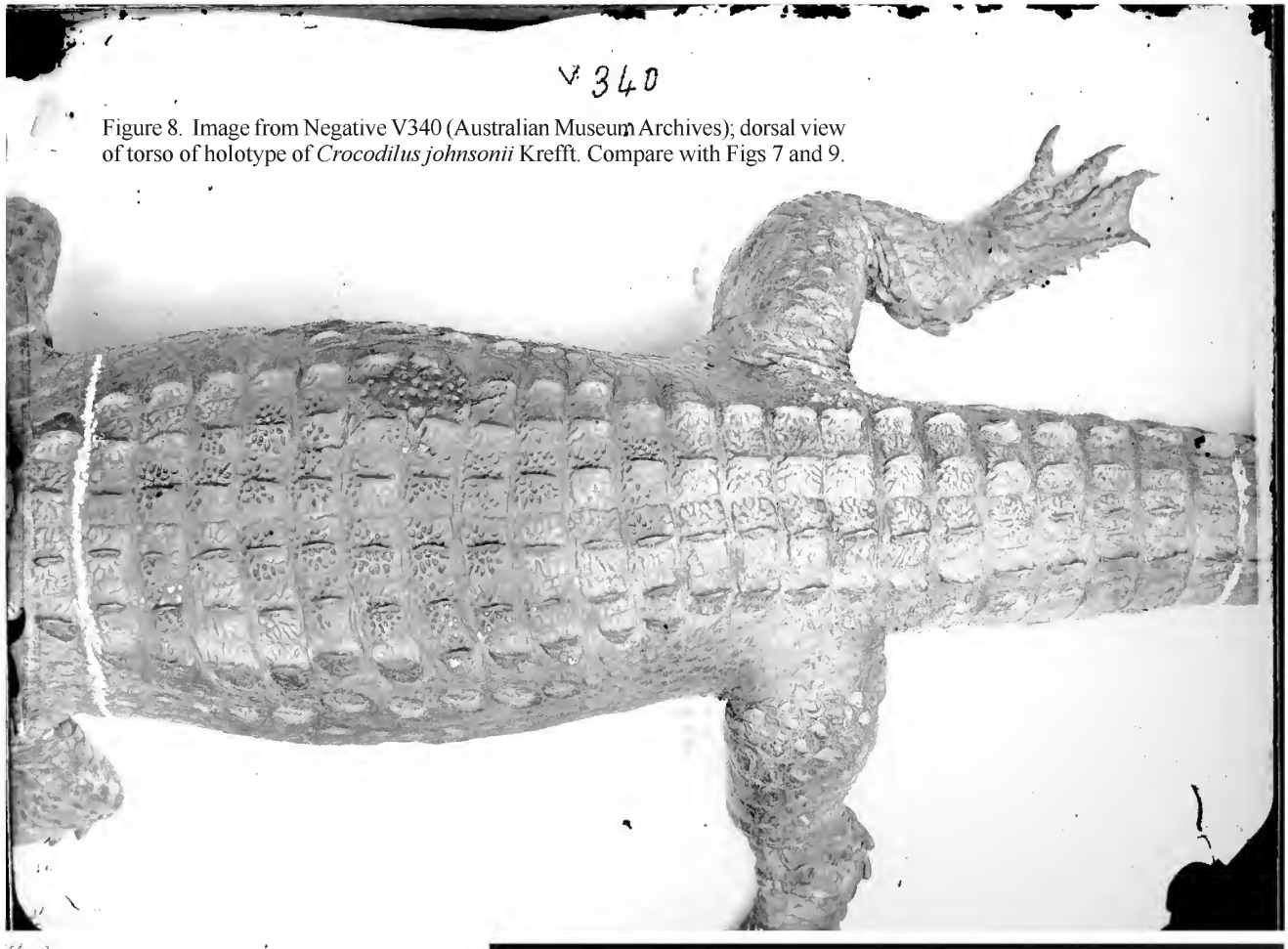

Figure 8. Image from Negative V340 (Australian Museum Archives); dorsal view of torso of holotype of *Crocodilus johnsonii* Krefft. Compare with Figs 7 and 9.

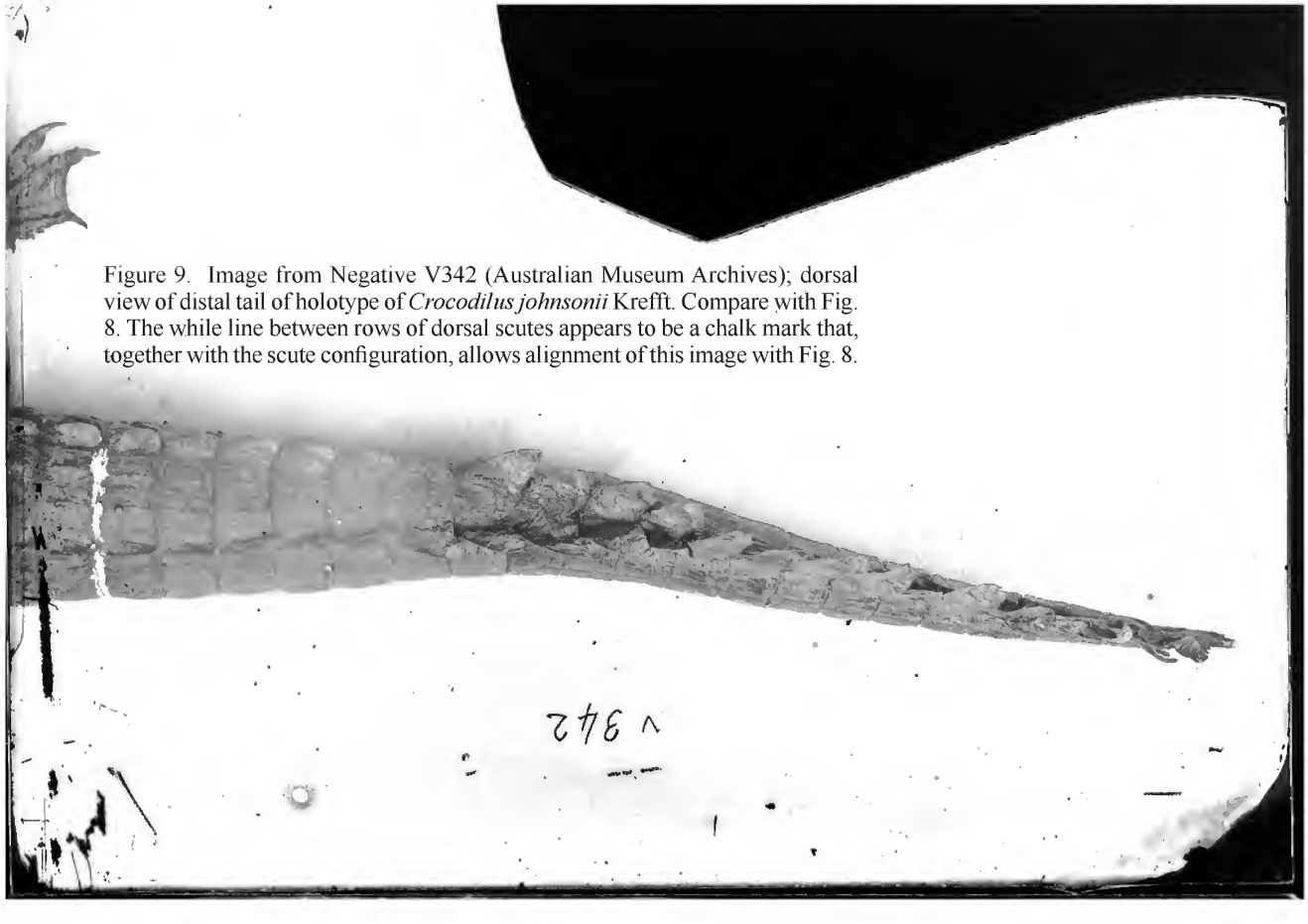

Figure 9. Image from Negative V342 (Australian Museum Archives); dorsal view of distal tail of holotype of *Crocodilus johnsonii* Krefft. Compare with Fig. 8. The while line between rows of dorsal scutes appears to be a chalk mark that, together with the scute configuration, allows alignment of this image with Fig. 8.

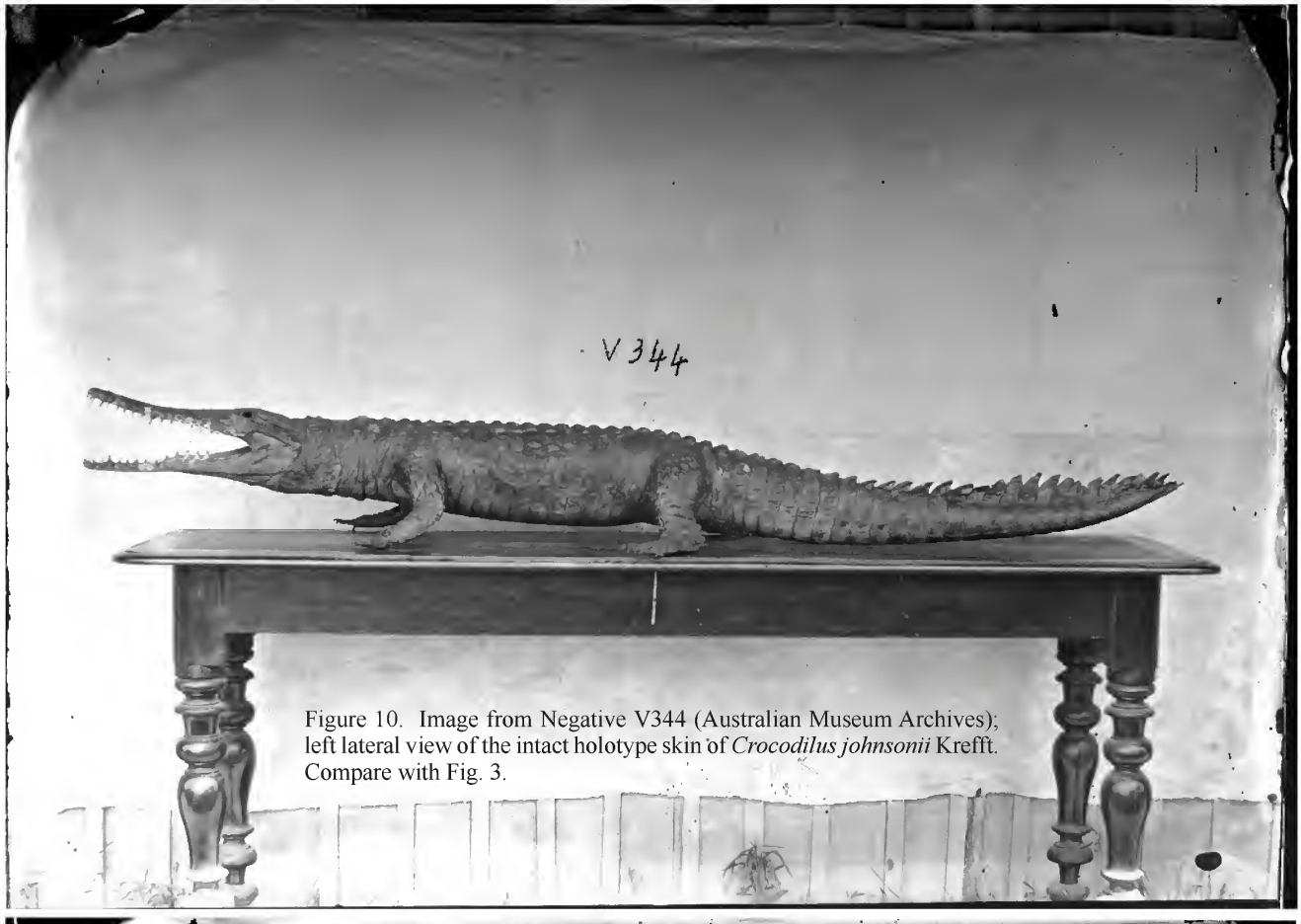

Figure 10. Image from Negative V344 (Australian Museum Archives); left lateral view of the intact holotype skin of *Crocodilus johnsonii* Krefft. Compare with Fig. 3.

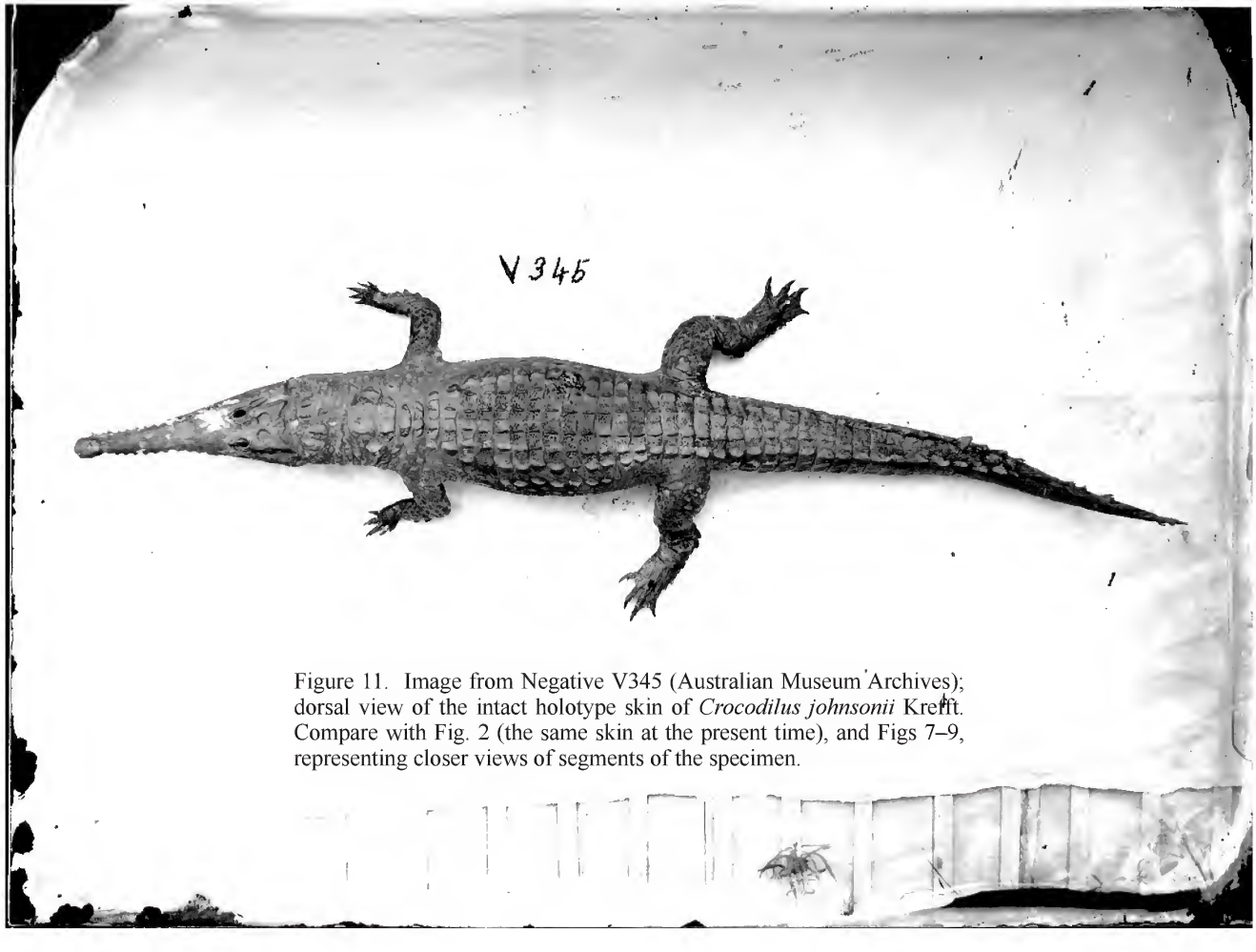

Figure 11. Image from Negative V345 (Australian Museum Archives); dorsal view of the intact holotype skin of *Crocodilus johnsonii* Krefft. Compare with Fig. 2 (the same skin at the present time), and Figs 7–9, representing closer views of segments of the specimen.

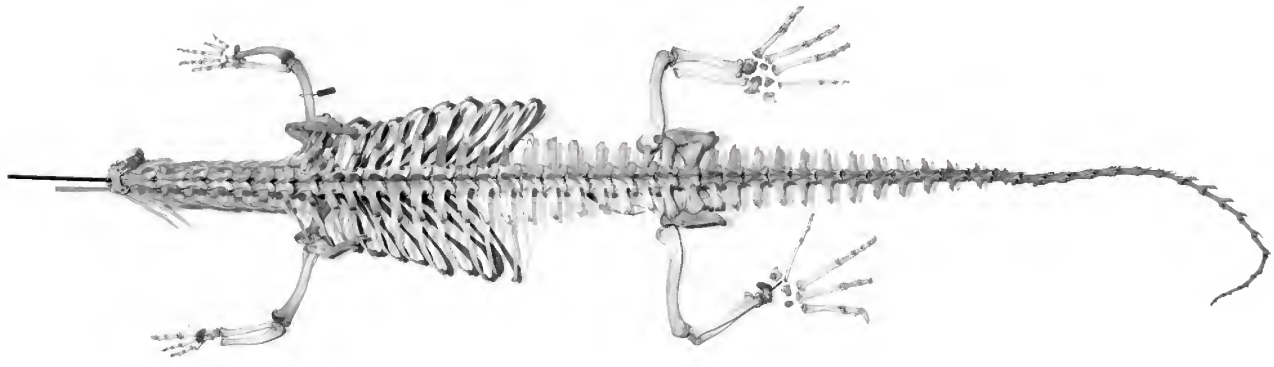

Figure 12. Dorsal view of the mounted skeleton AM R134548, purported to be from the same individual as the holotype skin of *Crocodilus johnsonii* Krefft.

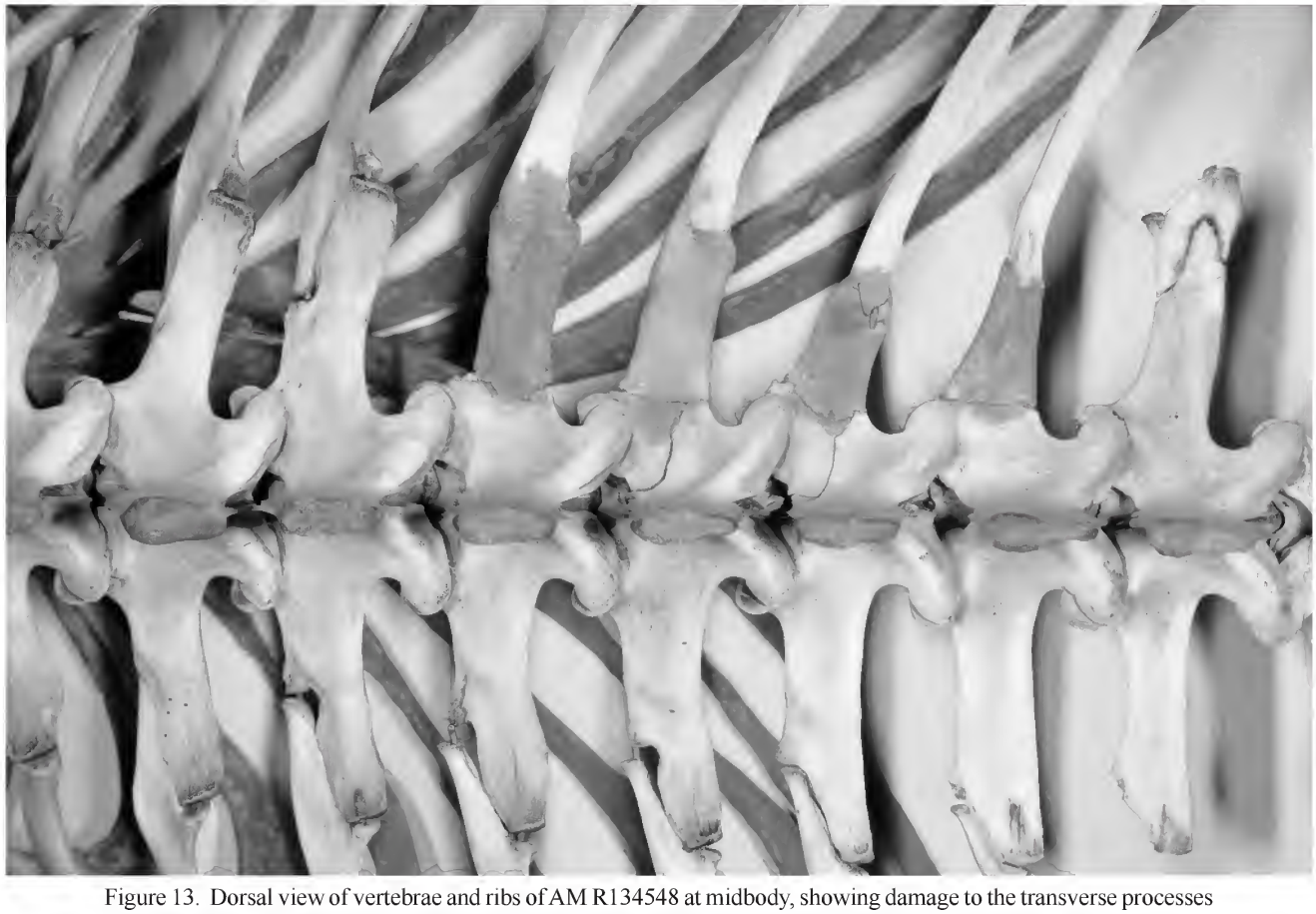

Figure 13. Dorsal view of vertebrae and ribs of AM R134548 at midbody, showing damage to the transverse processes and heads of ribs on right side, corresponding to the site of the presumed shot hole in the mounted skin.

comm.), and hence the photograph is likely to have come from a different collection, possibly the Australian Museum.

In the absence of the skull, is it possible to unequivocally link the postcranial skeleton to the skin, or if not, to the species? The general size and proportions of the postcranial skeleton match the skin, but there have been no detailed comparative anatomical studies of the postcranial osteology of the two Australian crocodile species that would allow certainty of identification. However, there is some forensic evidence that the skeleton and skin belong to the same specimen, additional to the information from Ramsay that was added to the original register entry by McCulloch. Johnstone (1904) reported that the holotype was shot by him. The holotype skin bears a repaired hole on the right side of the midline near midbody (Fig. 8) that presumably represents the damage made by the musket ball or rifle bullet. The skeleton has corresponding damage: the transverse processes on the right side of presacral vertebrae 15–18 and the heads of the corresponding ribs are missing, and have been replaced by sculpted artificial processes and rib heads (Fig. 13). The replacement transverse processes are noticeably shorter than real transverse processes on the left side, and those bordering the repaired area on the right side.

Hence, we accept that the skeleton, although not mentioned in any of the early literature associated with the species, does derive from the same specimen as the skin, and should be treated as part of the holotype. Forensic DNA studies may provide further evidence to support this argument.

The type locality of *Crocodilus johnsonii*

As presented in both descriptions of the species (Krefft, 1873a,b), the holotype was collected by Robert Johns[t]on from Cardwell, Rockingham Bay. The registration entry in the Palmer Register merely gives the locality as the upper Herbert River. However, several subsequent listings (e.g., Wermuth, 1953; Mertens & Wermuth, 1955; Wermuth & Mertens, 1961, 1977; Cogger *et al*., 1983; King, 1998) give the type locality as Cashmere on the upper Herbert River. This emendation would appear to have been derived from a quotation from the collector included with a description of the cranial osteology by Longman (1925), which states that Johnston shot the specimen in the Herbert River, near the mounted police camp at Cashmere. This in turn was stated by Longman to have been derived from a newspaper clipping. Longman did not provide details of which newspaper the quote came from, but it seems to be an extract from Johnstone (1904). Cashmere (18°08'13"S 145°20'20"E) is approximately 74 km WNW of Cardwell, it is the given type locality and a more likely locality for the species than Cardwell. It correlates well with Johnstone's 1871 assignment to Cashmere to be the Acting Sub-Inspector at the mounted police camp there and also with his observations that he shot several specimens, after the first, in the same stretch of water. Cardwell, the originally given locality, is near the coast and below the Herbert River Falls, an area which Johnstone did not consider the species to inhabit.

The collector and donor of the holotype of *Crocodilus johnsonii*

Both descriptions of the species (Krefft, 1873a,b) give the collector as Mr Johnson, and note that the specimen was sent by Johnson to a Mr C. Blaxland, jun., of Ryde, for Krefft's examination (Krefft, 1873a, further spells the donor's name as Bloxland). However, in the list of donations to the Museum for November–December 1872, the donor's name is given as J. G. Blaxland (Krefft, 1873c), and that version is also given in a later "Letter to the Editor" by Krefft reporting a large python sent by Johnstone to Blaxland for Krefft (Krefft, 1873d). The donor is either John Gregory Blaxland (8.x.1801–26.i.1884) of *The Hermitage*, Ryde, son of the explorer Gregory Blaxland, and aged 71 at the time of donation, or his eldest son, also John Gregory Blaxland (17.x.1846–12.xii.1906), and 26 years of age. The Australian Museum Archives has a letter (C.30.73) from Blaxland to Krefft, dated 13 January 1873 (two weeks after Krefft wrote his manuscript for the Zoological Society of London), that explains some of the details of the transfer:

> Ryde
> 13 Janry 1873
> Dear Krefft
> Your letter to me miscarried & I only received it last night—you addressed it to C. Blaxland J^{r}, whereas my name is John G. Blaxland. I am the donor of that specimen of the Crocodilus Johnsonii to the Museum—although I wished it named, as you have done, after the person who shot it—He is Sub Inspector of Police, at Cardwell—Rockingham Bay & his name is Robert Johnstone he takes great interest in natural history &c & if he collects any-thing rare will forward it to the Museum. He promised me this Crocodile a long time ago but when he sent it I thought I had better send it to you than try & preserve it myself—will you kindly have the card attached to it altered to "Presented by John G. Blaxland"
> & oblige
> Yours truly
> Jno. G. Blaxland."

Hence, while Krefft (1873a,b) initially gave the collector's name as Johnson, he was made aware of the error shortly after the newspaper account was published, and while the manuscript was *en route* to London. Krefft wrote to Gray on 15 May 1873 (while the description in the *ZSL Proceedings* was still awaiting printing), who published the correction early the following year (Gray, 1874), and Krefft himself, in his third article on Australian crocodiles (Krefft, 1874) also noted that the name was corrected to *johnstonii* "so as to indicate precisely the name of the discoverer". However, we, like Blaxland, note that the collector's name was Johnstone. He routinely spelt his name as Johnstone in his writings (e.g., Johnstone, 1904, and a number of other articles in the same series), and his biography in the *Australian Dictionary of Biography* is under the name Robert Arthur Johnstone (Jones, 1972).

What to do with the earlier names?

The existence of the earlier name *Crocodilus australis* Krefft, 1867 imperils the stability of nomenclature of *Crocodylus johnstoni*. Under the Code of Zoological Nomenclature, it is possible to reverse the priority of these two names, to maintain the usage of *C. johnstoni* to the species for which it has consistently been applied for almost 150 years (notwithstanding occasional use of the original spelling *johnsoni*—Tucker, 2010). Invoking Article 23.9, we note that *Crocodilus australis* has not been used as the available name for this species since it was first created by Krefft in 1867 (Article 23.9.1.1), while *Crocodylus johnstoni* has been used consistently as the available name for this species, including the following 25 papers and books published over the past 50 years, with more than 10 authors involved (Article 23.9.1.2): Britton *et al*. (2013), Campbell *et al*. (2010), Compton (1981), Firth *et al*. (2010), Grigg & Alchin (1976), Grigg & Kirschner (2015), Grigg *et al*. (2001), Hines & Skroblin (2010), Jamieson *et al*. (1997), Kennett & Christian (1993), Letnic & Ward (2005), Olsson & Phalen (2012), Renous *et al*. (2002), Richardson *et al*. (2002), Seebacher (1999), Smith & Phillips (2006), Somaweera *et al*. (2012), Taplin *et al*. (1982, 1999), Tucker *et al*. (2006), Walsh (1989), Webb & Manolis (1989), Webb *et al*. (1987), Whitehead & Seymour (1990), and Willis & Archer (1990). We further note that Grigg *et al*. (2001) is the edited proceedings of a conference, and contains 35 papers, of which 14, by a total of 27 authors, use the name *Crocodylus johnstoni*. Webb *et al*. (1987) is similarly an edited work based on a conference, containing 51 papers, of which 20, authored by various combinations of 20 authors, use *Crocodylus johnstoni*.

Hence, under Article 23.9, *Crocodilus australis* is a *nomen oblitum*, and cannot be used as the name for this species when both *C. australis* and *C. johnstoni* are considered conspecific.

However, it remains an available name, and should evidence arise that the populations to which the two names apply are not conspecific (or consubspecific), *C. australis* would become available for use for populations to the west of those represented by the type of *C. johnstoni* (Article 23.9.2, and associated Example).

Tomistoma krefftii, published simultaneously with *C. johnsonii* by Krefft (1873b), does not imperil stability of nomenclature, as it was placed in the synonymy of *C. johnsonii* by Krefft (1874), acting as First Revisor (Article 24.2). As it is a junior objective synonym of *Crocodilus australis* Krefft, it is permanently unavailable while *C. australis* remains available.

Krefft (1872, 1873b), in the two articles published in newspapers immediately after he wrote them (and hence unlikely to have been independently modified by scientific editors), and in the Museum's Annual Report for 1873 (Krefft, 1873e), used the *–ii* termination for the species epithet. This is contrary to the two papers that were published in the *ZSL Proceedings* (Krefft, 1873a; Krefft, in Gray, 1874), presumably without Krefft being able to see proofs of those papers, which used the single *-i* termination. This suggests that the *-ii* termination was his preference, and the *-i* orthography may have been an alteration to his manuscripts made by his London correspondents, particularly Gray. Under Article 33.4, and with recognition of the priority of the spelling by Krefft (1873b), the currently used *-i* form is to be considered an incorrect subsequent spelling, albeit one that, like the alteration of *johnsoni* to *johnstoni*, is now in general usage, and consequently, under Article 33.3.1, is to be maintained.

While the Code allows for reversal of priority of the name *Crocodilus australis* Krefft, 1867 and *Crocodilus johnstoni* without recourse to use of the Plenary Powers of the Commission, the same is not true for the primary and secondary homonymies created by the discovery of *C. australis* Krefft, due to the lack of use of the subsequent three *australis* epithets among crocodilians: *Crocodilus australis* Bravard, in Burmeister, 1885 has been rarely mentioned in the literature, although consistently recognized as a valid species of alligatorid when it is mentioned; *Oophilus porosus* var. *australis* Günther, in Gray, 1867 has been overlooked by all subsequent authors, and *Crocodylus porosus australis* Deraniyagala, 1953 has remained in synonymy (of either *C. porosus* or *Alligator mississippiensis*) since 1960, and hence none fulfill Article 23.9.1.2. In order to maintain usage of *Crocodilus australis* Bravard, in Burmeister, and to remove the secondary homonymy with *Oophilus porosus* var. *australis* Günther, in Gray within *Crocodylus*, a request to the ICZN should be prepared to suppress *C. australis* Krefft for the purposes of homonymy, or a replacement name be provided for the fossil caiman. We leave this to specialists in South American alligatorid palaeontology to decide.

We summarise the findings of our paper with the following synonymy for *Crocodylus johnstoni*:

Crocodylus johnstoni Krefft, 1873

Crocodilus australis Krefft, 1867, *The Australasian* (new series) 3(69): 8 (*nomen oblitum* with respect to *Crocodilus johnstoni*, action taken here under Article 23.9 of the Code of Zoological Nomenclature).

Holotype: a skull donated to the Australian Museum, lost, collected by William Wood.

Type locality: Gulf of Carpentaria (actual place of capture, the hinterland of Burketown, based on collector's known movements).

Not *Oophilus porosus* var. *australis* Günther, in Gray, 1867, *Transactions of the Zoological Society of London* 6: 138 (now in synonymy of *Crocodylus porosus*); not *Crocodilus australis* Bravard, in Burmeister, 1885, *Anales del Museo Nacional de Buenos Aires* 3(2): 148 (now *Caiman australis*); not *Crocodylus porosus australis* Deraniyagala, 1953, *A Colored Atlas of Some Vertebrates from Ceylon*, volume 2: 34 (now in synonymy of *Alligator mississippiensis*).

Crocodilus johnsonii Krefft, 1873, *Sydney Mail and New South Wales Advertiser* (new series) 15(653): 8.

Holotype: AM R134547, mounted skin, missing head; AM R134568, skeleton missing skull, Upper Herbert River, collected by R. Johnson [Johnstone], donated J. G. Blaxland.

Type locality: Cardwell, Rockingham Bay (corrected to Cashmere, upper Herbert River, by the collector—Johnstone, 1904).

Tomistoma krefftii Gray, in Krefft, 1873, *Sydney Mail and New South Wales Advertiser* (new series) 15(653): 8 (junior objective synonym of *Crocodilus australis* Krefft; synonymy with *Crocodilus johnsonii* by Krefft, 1874).

Holotype: as for *Crocodilus australis* Krefft.

Type locality: as for *Crocodilus australis* Krefft.

Crocodilus johnsoni Krefft, 1873, Proceedings of the Zoological Society of London 1873: 334 (incorrect subsequent spelling of *Crocodilus johnsonii* Krefft, 1873, *Sydney Mail and New South Wales Advertiser* [new series] 15[653]: 8).

Crocodilus johnstoni Krefft, in Gray, 1874, *Proceedings of the Zoological Society of London* 1874: 177 (emendation of *Crocodilus johnsoni* Krefft, 1873, *Proceedings of the Zoological Society of London* 1873: 334, preserved under Article 33.3.1 of the Code of Zoological Nomenclature).

Crocodilus johnstonii Krefft, 1874, *Sydney Mail and New South Wales Advertiser* 18(750): 630 (emendation of *Crocodilus johnsonii* Krefft, 1873, *Sydney Mail and New South Wales Advertiser* [new series] 15[653]: 8).

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Introduced Helicidae Garden Snails in Australia: Morphological and Molecular Diagnostics, Species Distributions and Systematics

MARK J. BLACKET,[1]* MICHAEL SHEA,[2] LINDA SEMERARO,[1] AND MALLIK B. MALIPATIL[1, 3]

[1] Department of Economic Development, Jobs, Transport and Resources (DEDJTR), Biosciences Research (BR), AgriBio, Centre for AgriBioscience, Bundoora Victoria 3083, Australia

[2] Australian Museum Research Institute, Sydney New South Wales 2010, Australia

[3] La Trobe University, Bundoora Victoria 3086, Australia

* mark.blacket@ecodev.vic.gov.au · http://orcid.org/0000-0001-7864-5712

ABSTRACT. There is a large number of Helicidae land snails native to the Western Palearctic, many of which have become invasive species in other parts of the world. In the past, multiple helicid species were introduced to Australia where they can now be major agricultural and horticultural pests. Determining which species have become established is essential for effective biosecurity and pest management. Here we have shown that three helicid species currently occur in Australia: Brown (*Cornu aspersum* Müller), Green (*Cantareus apertus* Born) and White (*Theba pisana* Müller) Garden Snails. A fourth formerly present species, the Chocolate Banded snail (*Eobania vermiculata* Müller) appears currently to be locally extinct. All four of these species are known to be highly invasive worldwide. Our study assessed the effectiveness of employing DNA barcoding for identification of garden snails in Australia through characterising DNA sequences of the mitochondrial Cytochrome Oxidase I and nuclear ITS2 loci. We were able to distinguish all four species, as well as other commonly intercepted Helicidae species. DNA sequences and diagnostic images of the helicid garden snails currently found in Australia have been added to the Barcode of Life Database (BOLD), as project AMPH (Australian Mollusc Pests—Helicidae), to aid in the identification of intercepted specimens, morphologically ambiguous individuals, or small juvenile specimens. We also examined the diagnostic morphological characters (juvenile and adult) that can be used to identify these species (including an illustrated key), and summarize relevant systematic and nomenclatural changes. We also provide the first specimen records for Green Garden Snails in eastern Australia, where they were previously unknown and may become a serious plant pest.

KEYWORDS. Land snails; Helicidae; introduced pests Australia; morphology; DNA barcoding; diagnostics; biosecurity.

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* author for correspondence

Members of Helicidae are land snails (Pulmonata: Stylommatophora) native to the Western Palearctic: Europe, Central Asia, the Middle East and Northern Africa, with more than 400 species currently recognised (Schileyko, 2006). Many species have expanded their ranges and are now cosmopolitan (Altaba, 2000; Cowie *et al.*, 2009; Peltanová *et al.*, 2012), including a number of species (Fig. 1) that have successfully established in Australia (Smith, 1992; Stanisic *et al.*, 2010), outlined further below. Introduced Helicidae species (garden snails) are associated with human activity, gardens and agriculture (Smith, 1992; Baker, 2002; Stanisic *et al.*, 2010), and can survive hot dry Australian summers through becoming dormant (aestivating). The pest status of Helicidae species in Australia is considered very severe, as they eat living plant material and are capable of causing extensive agricultural and horticultural damage (Kershaw, 1991; DAFWA, 2007; Stanisic *et al.*, 2010). Verifying which Helicidae species are currently present in Australia is essential for biosecurity and effective pest management.

The Brown Garden Snail, *Cornu aspersum* (Müller, 1774) (Figs 1, 2), is a cosmopolitan pest that has been repeatedly transported around the world (Guiller *et al.*, 2012; Peltanová *et al.*, 2012). This species was introduced to Australia soon after European settlement, possibly as a food source or imported accidentally in plant and soil material, from northern Europe (Smith, 1992). They were deliberately introduced into Tasmania (Petterd, 1879, cited in Petterd & Hedley, 1909) and in South Australia to eradicate slugs (Pomeroy & Laws, 1967). The Brown Garden Snail now occurs in all Australian states in many non-arid areas of southern and eastern Australia (Smith, 1992; Sanderson & Sirgel, 2002). The generic name of this species was recently under review, with debate as to whether it should be *Helix, Cornu, Cryptomphalus,* or *Cantareus* (Cowie, 2011), this species is currently recognized as *Cornu aspersum* (Stanisic *et al.*, 2010; ICZN, 2015).

Green Garden Snails, *Cantareus apertus* (Born, 1778) (Figs 1, 2), are also invasive worldwide (Godan, 1983; Cowie *et al.*, 2009). In Australia, they were first detected in the southwest coastal area of Western Australia in the 1980's where they have maintained a restricted distribution localized near Perth through quarantine control (Smith, 1992; DAFWA, 2007), with interceptions on produce resulting in restricted movement of plant material (e.g., Medlen, 2016). Until recently, Green Garden Snails were unknown from eastern Australia. However, the present study documents the first records of Green Garden Snails from eastern Australia (see below).

Two other Helicidae species (Fig. 1), White Garden Snails (also known in Australia as White Italian Snails), *Theba pisana* (Müller, 1774) and Chocolate Banded Snails, *Eobania vermiculata* (Müller, 1774), have also been introduced to Australia (Stanisic *et al.*, 2010). Both species are highly invasive worldwide (Deisler *et al.*, 2001; Roth & Sadeghian, 2003; Ueshima *et al.*, 2004; Cowie *et al.*, 2009; Neiber *et al.*, 2011). In Australia, *T. pisana* is currently present in all southern states, where it is a major grain (Baker, 2002), pasture (Baker, 2002) and grapevine (Sanderson & Sirgel, 2002) pest, with the major damage caused being contamination of harvested produce. The final helicid species, *E. vermiculata,* became established near Sydney, but now appears to be locally extinct (Stanisic *et al.*,

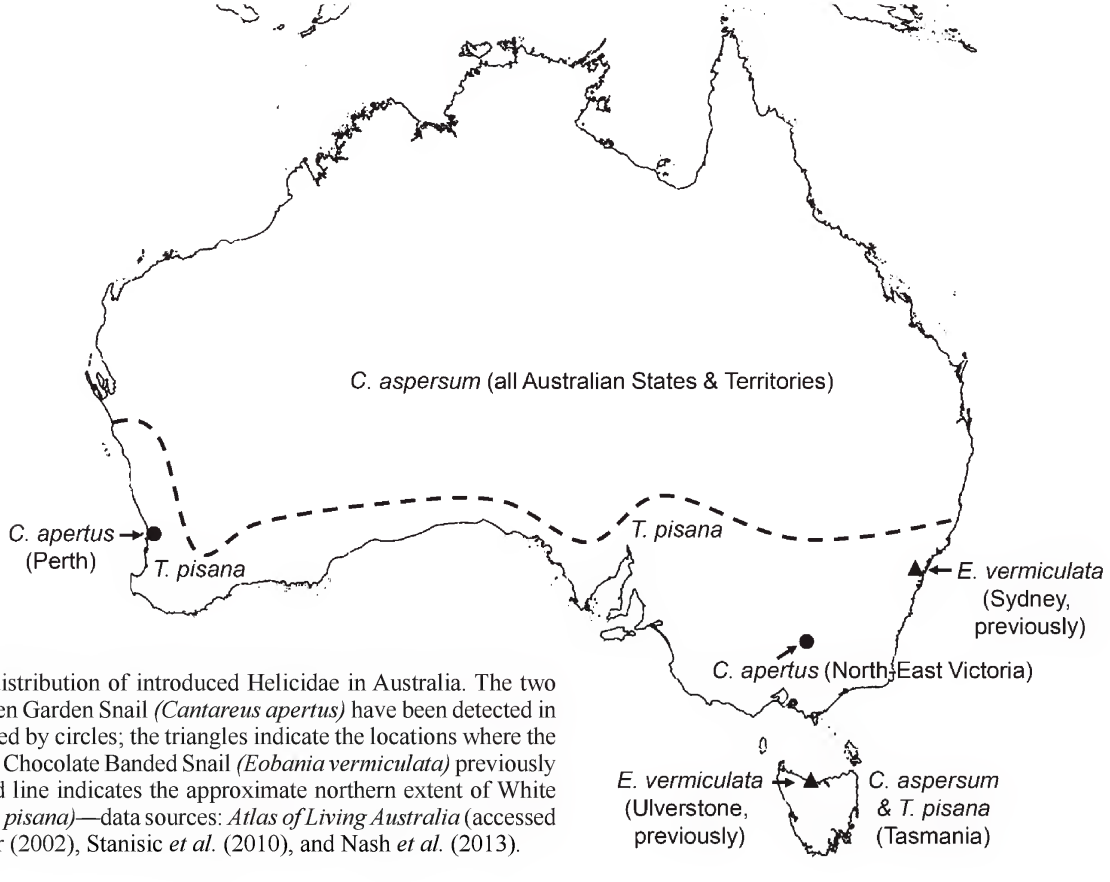

Figure 1. Current distribution of introduced Helicidae in Australia. The two locations where Green Garden Snail *(Cantareus apertus)* have been detected in Australia are indicated by circles; the triangles indicate the locations where the (now locally extinct) Chocolate Banded Snail *(Eobania vermiculata)* previously occurred; the dashed line indicates the approximate northern extent of White Garden Snail *(Theba pisana)*—data sources: *Atlas of Living Australia* (accessed March, 2015), Baker (2002), Stanisic *et al.* (2010), and Nash *et al.* (2013).

Figure 2. Images of live Brown *(C. aspersum)* and Green *(C. apertus)* Garden Snails. *(A)* Brown adult, Knoxfield Vic.; *(B)* Green adult, Cobram Vic.; *(C)* Brown adult, Knoxfield Vic. (left) and Green adult, Cobram Vic. (right); *(D)* Brown juvenile, Knoxfield (left ×1) and Cobram (right ×2) [note: these three specimen identifications (VAITC 3071–3073) were confirmed through DNA barcoding in the present study]; *(E)* Green Juvenile, Cobram Vic.; *(F)* Green epiphragm, Cobram Vic. Image credits: A–E, Andrew Henderson (DEDJTR); F, Gordon Berg (DEDJTR).

2010), with no specimens detected since the 1980's (Shea *et al., unpublished data*). Interestingly *E. vermiculata* has also been recorded as being abundant in northern Tasmania in the past (Petterd & Hedley, 1909), where it was formerly known from Leven River, Ulverstone Tasmania, but apparently no longer occurs there (K. Bonham, pers. comm.).

In addition to the four species outlined above, literature records suggest that a number of other Helicidae species may have established in Australia (Table 1). Smith (1992), listed the Milk Snail, *Otala lactea* (Müller), from Sydney and suggested that it is highly probable that Escargot, *Helix pomatia* (Linnaeus), might be present in Australia illegally for commercial purposes. Literature records suggest that Green Garden Snails have been found in Tasmania (Petterd & Hedley, 1909; Kershaw, 1991), however, this appears to be due to a nomenclatural error (see *Discussion*). Indeed, there have been a large number of recent nomenclatural changes, including recognition that many introduced snails previously regarded as Helicidae actually belong to Hygromiidae and Cochlicellidae (Table 1). Currently, seven species (in six genera) of Helicidae are listed as being "Recorded in Australia" based on museum records on the *Atlas of Living Australia* (ALA, http://www.ala.org.au/, accessed March 2015), including specimens of *Cepaea nemoralis* (Linnaeus), *Helix pomatia,* and *Otala lactea*, see Table 1. However it is, in many cases, unclear if these records represent specimens collected overseas housed in Australian collections, interceptions of exotic species at the nation's borders, or the establishment of particular species in Australia.

Morphological identification of Helicidae species can be difficult, with forty-four families of native terrestrial snail known from eastern Australia (Stanisic *et al.,* 2010), and an additional forty (Smith, 1992) to fifty (Sanderson & Sirgel, 2002) exotic species established in Australia. The large degree of morphological variation present in some snail species can make identification of morphologically similar species problematic, especially for juvenile specimens. Potentially DNA barcoding could aid in snail identification, however, it is essential that reference DNA sequences match vouchered specimens. Indeed, many Helicidae DNA sequences on GenBank have been shown to have been previously assigned to incorrect species (Groenberg *et al.,* 2011).

The three major aims of the present study were: *(a)* to review which Helicidae species have become established in Australia through an examination of literature and specimen records; *(b)* to examine diagnostic characters, both morphological (juvenile and adult) and molecular, to allow identification of Helicidae species in Australia; and *(c)* to provide a formal first record for Green Garden Snails from eastern Australia.

Materials and methods

Specimens examined

Juvenile and adult Australian specimens of four introduced Helicidae species: *Cornu aspersum*, *Cantareus apertus*, *Theba pisana*, and *Eobania vermiculata*, were examined morphologically (specimen details given in Table 2, and *Systematics* section). A series of Victorian specimens of *C. apertus* (from near Cobram), *C. aspersum* and *T. pisana* were examined for molecular variation (Table 2, n = 23), see below. The shells of these specimens were photographed with a Canon 5D digital SLR camera. Diagnostic images and associated DNA sequences are presented (this study) and have been submitted to the Barcode of Life Database (BOLD) as project AMPH: Australian Mollusc Pests—Helicidae. Specimens examined for molecular variation were prepared by freezing overnight, followed by removal of the body in 100% ethanol; specimens relaxed for morphological

examination of the soft body were prepared as in Stanisic *et al.* (2010), and preserved in 70% ethanol. Reference collection abbreviations: *AM*, Australian Museum; *VAIC*, Victorian Agricultural Insect Collection; *VAITC*, Victorian Agricultural Insect Tissue Collection (the VAIC and VAITC collections also include molluscs and other invertebrates).

Morphological variation

Six shell measurements were taken from Australian specimens of all four Helicidae species, from the axial-aperture view, as in Fig. 3 (specimens listed in Table 2, n = 89): *(1)* SW: shell width; *(2)* AW: aperture width, from the edge of columellar plait to edge of lip; *(3)* SH: shell height; *(4)* BW: height of body-whorl; *(5)* AH: aperture height, from the point of adhesion of aperture to edge of lip; *(6)* W: height of whorls (excluding the body-whorl), calculated from SH–BW measurements. All measurements, to the nearest 0.1 mm, were obtained using electronic digital callipers. Statistical tests, Discriminant Function Analyses and Principal Component Analyses, were performed using XLSTAT 2015 in Excel 2010 to assess differences between species and lifestages (note, in the present study there were no very small *E. vermiculata* available for examination). The general morphology of the shell and the soft body—the mantle, head and foot—were also examined for potential interspecific size, colour and pattern differences (in *E. vermiculata* only shells were available).

Molecular variation

DNA extractions were performed on approximately 3 mm^2 of foot tissue removed from ethanol preserved specimens with a single-use scalpel blade, using a commercially available kit (Dneasy® Blood and Tissue Kit, Qiagen), following the manufacturers protocol. Genetic variation was examined in two loci, the mitochondrial Cytochrome Oxidase I (COI) locus, and the nuclear Internal Transcribed 2 (ITS2) region. COI was amplified using primers LCO / HCO (Folmer *et al.,* 1999) as in Régnier *et al.* (2011), while novel ITS2 primers, Snail_ITS2-F (5'-GACATCTTGAACGCAMATGG-3') and Snail_ITS2-R (5'-TCACTCGCCGTTACTGRGG-3'), were designed using Primer 3 (Rozen & Skaletsky, 2000) to match Helicidae sequences on GenBank (from Wade et al., 2001, 2006), to amplify the ITS2 region, overlapping with data from Wade *et al.* (2001, 2006) and Colomba *et al.* (2011). PCR profiles for both loci involved an initial denaturation step of 94°C for 2 minutes, 40 amplification cycles of 30 second steps (at 94°C, 52°C and 72°C for COI, and 94°C, 55°C and 72°C for ITS2), and a final extension step of 72°C for 2 minutes. DNA sequencing was conducted commercially through Macrogen Inc. (Korea). The COI and ITS2 sequences obtained here have been submitted to GenBank (Table 2).

Blastn searches of both COI and ITS2 DNA sequences were conducted on NCBI GenBank to determine the closest species match for each DNA sequence. Additional estimates of COI variation and relationships between species / genera (using a Neighbour-joining tree, pairwise "p" sequence distances) were conducted in MEGA version 6 (Tamura *et al.,* 2013), including a sequence representative from many of the Helicidae genera currently available on GenBank (from Ansart *et al.* [unpublished *Helix, Cantareus*]; Däumer *et al.,* 2012; Dinapoli *et al.,* 2010; Elejalde *et al.,* 2008; Grande *et al.,* 2004; Greve *et al.,* 2010; Grindon & Davidson, 2013; Groenenberg *et al.,* 2011; Haase & Misof, 2009; Kotsakiozi *et al.,* 2012; Neiber *et al.,* 2011; Rada *et al.,* 2012; Régnier *et al.,* 2011). Phylogenetic analyses of the ITS2 sequences obtained in the present study were not conducted, due to the presence of a large number of alignment gaps between species and indels within species (see below).

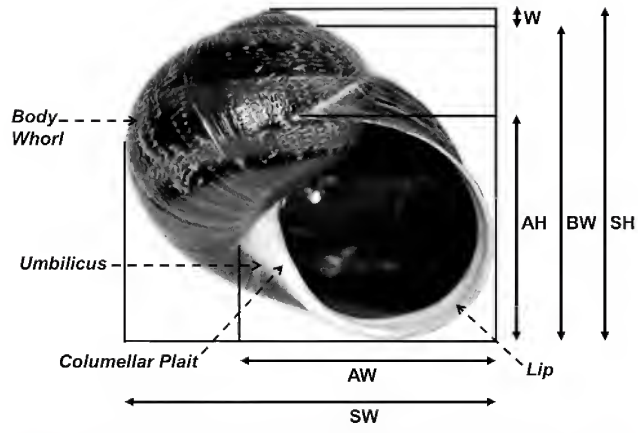

Figure 3. Snail shell with characters mentioned in the text labelled (dashed arrows). Locations of shell measurements are indicated by solid arrows and lines. *Abbreviations: AH:* aperture height; *AW:* aperture width; *BW:* body-whorl height; *SH:* shell height; *SW:* shell width; *W:* height of whorls, calculated from SH–BW.

Results

Helicidae species present in Australia

In the present study three Helicidae species were verified as being currently established in Australia: *C. aspersum*, *C. apertus*, *T. pisana*. A fourth species, *E. vermiculata,* became locally established twice, in NSW and Tasmania, but now appears locally extinct in both locations. No evidence for any additional species in Australia referred to in previous literature (see above and Table 1) were found. Indeed, reference collection specimens were not located in the present study to support previous literature records for *E. vermiculata* from northern Tasmania (Petterd & Hedley, 1909) or for *O. lactea* from NSW (Smith, 1992). It appears likely that previous NSW records of *O. lactea* were actually misidentified *E. vermiculata* (Shea, unpublished data) and that *E. vermiculata* was formerly known from northern Tasmania (K. Bonham, pers. comm.), but is not represented in reference collections. A number of other exotic Helicidae species are regularly intercepted at the nation's border (e.g., Table 3), with more than 900 interceptions occurring between 2002 and 2015, including at least 14 different Helicidae species (L. Watson, pers. comm.); however, none of these are known to have led to additional Helicidae species becoming established in Australia. Images, and adult shell sizes, of some exotic species commonly misidentified or intercepted at the border are shown in Fig. 4.

Morphological identification of Helicidae in Australia

Most native terrestrial snail species are small, subglobose, and not domestic in habit (Kershaw, 1991; Smith, 1992; Stanisic *et al.,* 2010). An up-to-date family key for eastern Australia is available to aid in identification (Stanisic *et al.,* 2010). A number of introduced species of Hygromiidae and Bradybaenidae are morphologically and ecologically similar to species of Helicidae (Stanisic *et al.,* 2010). Bradybaenidae is currently represented by a single species in Australia, the Asian Trampsnail *Bradybaena similaris* (illustrated in Stanisic *et al.,* 2010). Hygromiidae is a large Western Palearctic family with numerous species now established in Australia (e.g., Smith, 1992; Stanisic *et al.,* 2010). Hygromids vary widely in shell shape, but their shells do not usually possess a reflected lip or have a differentiation between the lip edge and the columella, the external soft body is similar in appearance to Helicidae but usually has a narrower foot (Stanisic *et al.,* 2010). Other more detailed descriptions of diagnostic Helicidae/Hygromiidae characters are outlined in Schileyko (2005, 2006), and a large number of potential exotic species are covered by Welter-Schultes (2012).

Some native snails, including many species of Camaenidae, which is one of the largest families in Australia and the dominant group in the tropics, could potentially be confused with Helicidae snails in being both globose and large in size (Stanisic *et al.* 2010). Species of Camaenidae differ from Helicidae/Hygromiidae in not possessing a dart sac and in having an eversible "head wart" (which emits an attractant pheromone) situated between the two superior tentacles (Stanisic *et al.,* 2010).

Specimens of the four Helicidae Garden Snail species collected from Australia, that are larger than c. 10 mm in diameter (specimens smaller than this often have fewer whorls and variable coloration), can be identified using the diagnostic images presented here (Figs 2, 5–7) and the following key:

Key to Helicidae species in Australia

1 Shell globose, with whorls increasing rapidly in width, 3–5 whorls, body-whorl greatly flared, aperture large and rounded, umbilicus closed, shell colour brown or green either with brown spiral bands or without a pattern (Figs 5–7, A and B) 2

—— Shell subglobose, with whorls increasing gradually in width, 5 whorls, body-whorl moderately flared, aperture small to medium, umbilicus narrow or closed, shell colour pale with brown spiral bands (Figs 5–7, C and D) 3

2 Shell large size (up to 4 cm in diameter, axial view), light brown colour with darker spiral bands and yellow flecks, raised spire, 4–5 whorls, aperture large relative to body. In adults spire more developed and lip of shell thickened white and strongly reflected out. During aestivation possesses either thin and clear or thickened and greyish green epiphragm that is not convex positioned inside aperture (Figs 2, 5–7, A) ..... *Cornu aspersum*

—— Shell medium size (up to 3 cm in diameter, axial view), olive-green (juveniles) to olive-brown (adults) colour with no banding pattern, low spire, 3–4 whorls, aperture extremely large relative to body. In adults lip of shell only thickened and white internally and not reflected out. During aestivation possesses distinctive convex white thick epiphragm (Fig. 2F) extending from edge of aperture (Figs 2, 5–7, B) ..... *Cantareus apertus*

3 Shell relatively depressed, medium size (up to 3 cm in diameter, axial view), light brown to yellow usually with continuous thick dark brown and white spiral bands and yellow flecks, rounded whorls, usually closed umbilicus, aperture small compressed shape. In adults lip of shell thickened white and strongly reflected out (Figs 5–7, C) ..... (locally extinct) *Eobania vermiculata*

—— Shell relatively tall, small size (up to 2 cm in diameter, axial view), white usually with broken thin dark brown spiral bands and chevrons, whorls angulate in juveniles rounded in adults, narrow umbilicus, aperture medium size rounded. In adults lip of shell internally thickened and pink not thickened externally or reflected out (Figs 5–7, D) ..... *Theba pisana*

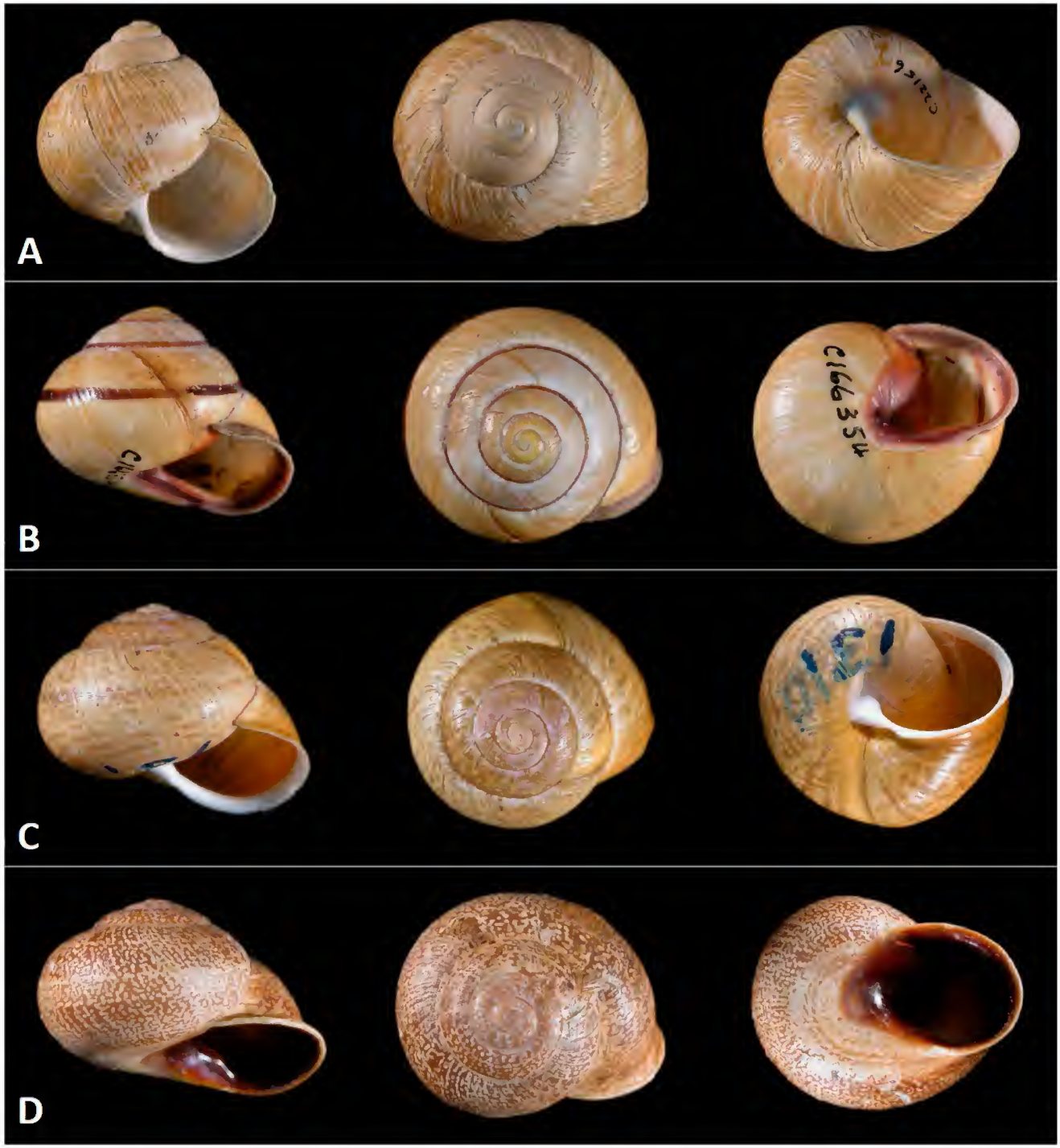

Figure 4. Some exotic species of Helicidae commonly misidentified and/or intercepted at the Australian border. *(A) Helix pomatia* (AM C22156), SW=30–50 mm; *(B) Cepaea nemoralis* (AM C166354), SW=18–25 mm; *(C) Arianta arbustrorum* (AM unregistered England), SW = 18–25 mm; *(D) Otala lactea* (AM unregistered, Portugal), SW = 30–40 mm. (Images are adults, not shown to same scale). Image credits: A–D, Des Beechey (AM).

Shell morphology

As well as the characters listed above, many shell size measurements appear different between the four species of garden snail (Table 4). Principal Component Analyses indicate that all variables contribute to differences between species (Table 4). However, most shell traits appear strongly correlated with each other (correlations >0.7, tolerance statistic <0.05), which is probably due to correlations of each trait with size (Table 4). Moderate correlations (0.49–0.52) were observed between trait W with AH and BW, reflecting between-species differences in shell shape (Fig. 8). Bivariate plots of shell measurements differ for each species (Fig. 8), with some relative proportions showing almost no overlap between species, or between conspecific adults and juveniles (Fig. 8). Discriminant Function Analyses of shell measurements (Table 4) indicated that most (>90%) specimens could be statistically assigned to the correct species and lifestage, based on confusion matrix estimates. Instances of incorrect assignment of specimens involved a number of juvenile *C. aspersum* (×2) and *C. apertus* (×2) specimens assigned as juveniles of the other species, and assignment

Table 1. Taxa that were regarded as Helicidae in selected past Australian field guides and checklists. Grey shading indicates that a species was not included in that particular geographically-localised reference, dashes indicate that species was included but not as Helicidae. Geographic regions in square brackets.

	Smith & Kershaw (1979) [S.E. Australia]	Kershaw (1991) [Tasmania]	Smith (1992) [Australia]	Stanisic *et al.* (2010) [Eastern Australia]	ALA[c] (2015) [Australia]	present in Australia	snail family (2015)
Brown Garden Snail	*Helix (Cryptomphalus) aspersa*	*Helix (Cryptomphalus) aspersa*	*Helix (Cornu) aspersa*	*Cornu aspersum*	*Cantareus aspersa* (Müller, 1774)	yes	Helicidae
Green Garden Snail		*Cantareus aperta*	*Helix (Cantareus) aperta*		*Cantareus apertus* (Born, 1778)	yes	Helicidae
Chocolate Banded Snail	*Eobania vermiculata*		*Eobania vermiculata*	*Eobania vermiculata*	*Eobania vermiculata* (Müller, 1774)	formerly	Helicidae
White Garden Snail	*Theba pisana*	*Theba pisana*	*Theba pisana*	*Theba pisana*	*Theba pisana* (Müller, 1774)	yes	Helicidae
Milk Snail			*Otala (Otala) lactea*		*Otala (Otala) lactea* [a] (Müller, 1774)	no [a]	Helicidae
Pointed Snail	*Cochlicella acuta*		*Cochlicella acuta*		*Cochlicella acuta* (Müller, 1774)	yes	Cochlicellidae
Small Pointed Snail	*Cochlicella ventrosa*	*Cochlicella barbara*	*Cochlicella barbara*	—	*Prietocella barbara* (Linnaeus, 1758)	yes	Cochlicellidae
Vineyard Snail	*Cernuella (Cernuella) virgata*		*Cernuella (Cernuella) virgata*	—	*Cernuella (Cern.) virgata* (Da Costa, 1778)	yes	Hygromiidae
Citrus Snail [b]	*Cernuella (Microxeromagna) vestita*	*Cernuella (Microxeromagna) vestita*	*Cernuella (Microxeromagna) vestita*	—	*Microxeromagna lowei* (Potiez & Michaud, 1838)	yes	Hygromiidae
Dune Snail	*Cernuella (Xerocinta) neglecta*	*Cernuella neglecta*	*Cernuella (Xerocinta) neglecta*	—	*Xerocincta neglecta* (Draparnaud, 1805)	yes	Hygromiidae
Wrinkled Dune Snail	*Candidula intersecta*		*Candidula intersecta*		*Candidula intersecta* (Poiret, 1801)	yes	Hygromiidae

a Note: *Otala lactea, Helix pomatia* and *Cepaea nemoralis* are all currently listed on the *ALA* (accessed March 2015) as "Recorded in Australia". However, these appear to refer to intercepted specimens, with these species not currently established in Australia.

b Note: Citrus snail is missing from the ALA (accessed March 2015), but is currently recognized as *Microxeromagna lowei* (Potiez & Michaud, 1838).

c ALA = Atlas of Living Australia · http://www.ala.org.au

Table 2. Number of adult and juvenile specimens examined for morphological measurements, molecular variation and DNA barcoding. Asterisks indicate collection localities for specimens photographed in Figs 2, 5–7.

species	location	adults	juveniles	GenBank accession no. (COI)	GenBank accession no. (ITS2)
Cornu aspersum	Doncaster, Vic	2	1 *	KX679317	KX679294
	Irymple, Vic	3 *	8 *	KX679314, KX679322	KX679292, KX679299
	Knoxfield, Vic	—	7	KX679320	KX679297
	Preston, Vic	—	4	KX679321	KX679298
	Ringwood East, Vic	1 *	4	KX679319	KX679296
	Blackburn South, Vic	—	1 *	KX679318	KX679295
	Cobram, Vic	—	2 *	KX679315, KX679316	KX679293
Cantareus apertus	Neerabup, WA	—	2	N/A	N/A
	Cobram, Vic	2 *	8 *	KX679306, KX679307, KX679308, KX679311	KX679284, KX679285, KX679286, KX679289
	Cobram South, Vic	—	9 *	KX679309, KX679310, KX679312, KX679313	KX679287, KX679288, KX679290, KX679291
Eobania vermiculata	Bronte, NSW	18 *	—	N/A	N/A
	Ryde, NSW	—	4 *	N/A	N/A
	Ryde, NSW	—	4 *	N/A	N/A
Theba pisana	3 km N Port Campbell, Vic	3	—	N/A	N/A
	Port Campbell, Vic	3	—	N/A	N/A
	Venus Bay, Vic	5 *	5 *	KX679323 – KX679328	KX679300 – KX679305

of one juvenile *E. vermiculata* as an adult *T. pisana*, with an additional four specimens within these latter two species assigned to the incorrect lifestage. In all species juvenile specimens appear generally paler in colour, possess a thinner shell-lip and have relatively lower spires than adults (Figs 2, 5–8). The degree of development and angle of the columellar plait also differs between species (Fig. 5), particularly in adult *E. vermiculata* where it occurs at a very shallow angle.

The colour and pattern of garden snail shells is extremely variable, and may be related to geographic and/or ecological factors (Johnson, 1980). Baker (2002), has previously reported that the shells of South Australian *T. pisana* are commonly entirely white. Indeed, it has been well documented that some helicid species that are normally patterned can have non-banded forms, e.g., *T. pisana*—Deisler *et al.,* 2001 and *E. vermiculata*—Yildirim, 2004. In the present study specimens examined were patterned as described in the above key.

Of the four species examined Brown and Green Garden Snails appear most similar and can be very difficult to identify as juveniles (Fig. 2). Indeed, in the present study reliable identifications of very small specimens of these two species were only possible through DNA barcoding (e.g., Fig. 2D). In addition to being non-banded with lower spires (Figs 5 and 8D), adult and juvenile *C. apertus* were found to consistently have larger apertures compared with *C. aspersum* specimens, with AH proportionally larger (Fig. 5, Fig. 8B AH:SW, Fig. 8C AH:AW). Relative aperture size is known to affect desiccation resistance in snails (Perrot *et al.,* 2007), and the large-apertured Green Garden Snails burrow freely into soil and seal their shells with a strong white coloured epiphragm (see Fig. 2F) during drought aestivation (Kershaw, 1979; DPI, 2011), while the other three smaller-apertured species *(C. aspersum, T. pisana, E. vermiculata)* generally seal their shells against vegetation and other objects (Baker, 2002; Yildirim, 2004; Stanisic *et al.,* 2010). A further distinguishing feature of living Green Garden Snails is the characteristic noise they often make when disturbed (Schultes, 2012).

Mantle, head and foot morphology

The soft body of adult garden snails generally appears darker than juveniles, and the surface develops rough tubercles with age (see Fig. 2). The colour of the soft body can be variable within species, however, generally, *C. aspersum* are greenish-grey with a pale dorsal stripe (Fig. 2); *C. apertus* are variably light or dark, but are often cream coloured, with dark dorsal stripes (Fig. 2); *E. vermiculata* are reported as being cream with a dark mantle (Stanisic *et al.,* 2010); while the soft body parts of *T. pisana* are pale overall.

Molecular variation

Comparisons of the DNA sequences obtained in the present study with sequences on GenBank (Blastn searches) revealed the most similar COI and ITS2 DNA sequences (< 5% difference COI, and < 3% difference ITS2) to be respectively with *C. aspersum, C. apertus* and *T. pisana*, confirming the morphological species identifications.

Several COI haplotypes were detected in *C. aspersum* and *C. apertus* (< 1.5% sequence divergence within each species), while only a single haplotype was found in the Victorian *T. pisana* (Fig. 9), which differed from the previous

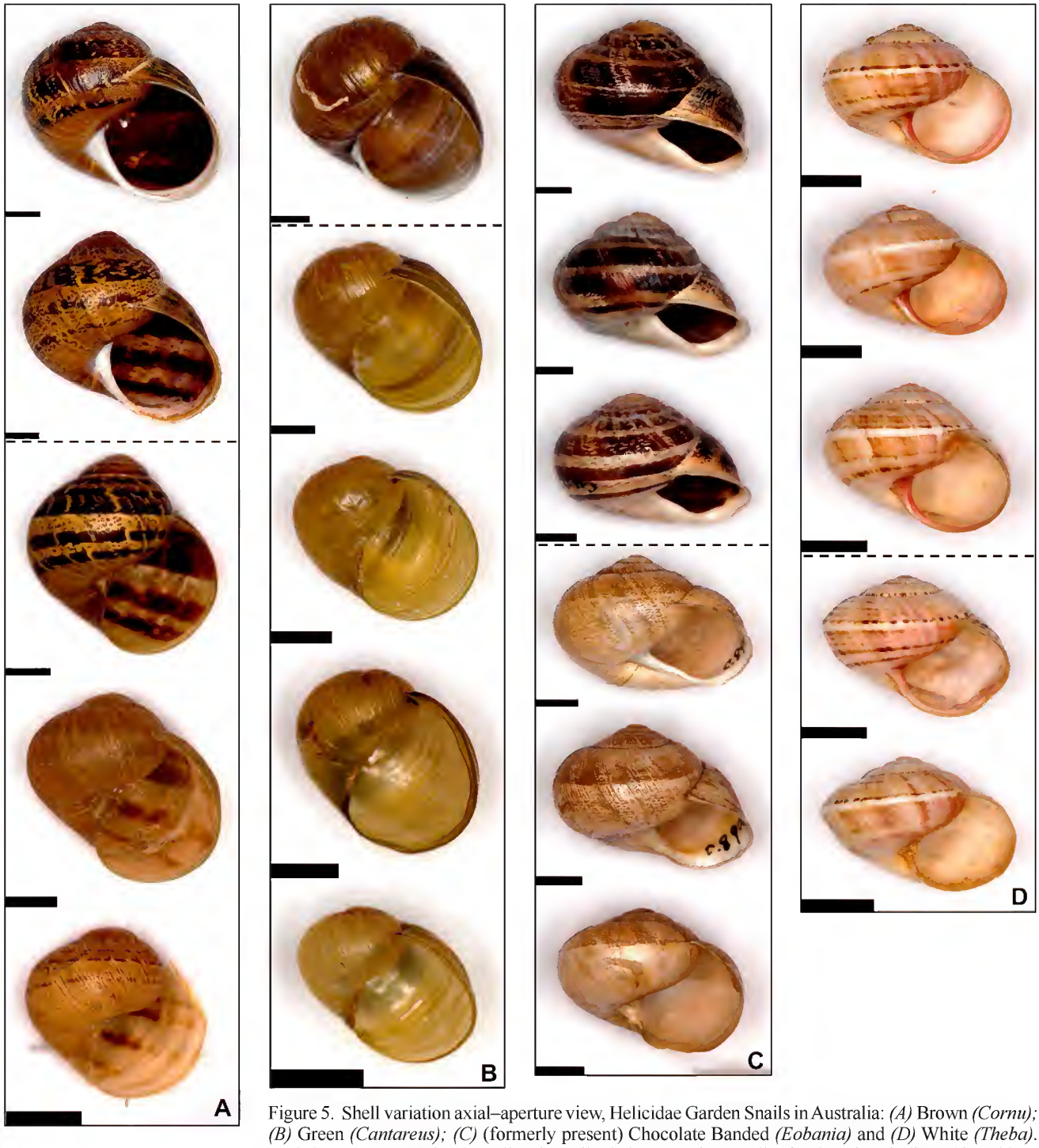

Figure 5. Shell variation axial–aperture view, Helicidae Garden Snails in Australia: *(A)* Brown *(Cornu); (B)* Green *(Cantareus); (C)* (formerly present) Chocolate Banded *(Eobania)* and *(D)* White *(Theba)*. Scale bar = 5 mm; adults above line, juveniles below; specimen collection locations indicated in Table 2.

T. pisana samples examined from Perth, Western Australia (Daumer *et al.*, 2012) by a single base. The ITS2 sequences obtained in the present study contained a small number of heterozygous bases, and were very similar within each species (< 1% divergent). Indels were present in ITS2 in all *C. aspersum*, half of the *C. apertus*, and none of the *T. pisana*; these indels prevented some small sections of the ITS2 sequences from being fully determined.

The COI DNA sequences obtained here for the "Universal" DNA barcoding region for *C. apertus* are the first to be obtained for this species and submitted to BOLD. Currently there is also a single unpublished sequence for this species on GenBank (JX911286, from an unspecified collection locality) which is > 4% divergent from the sequences obtained in the present study (Fig. 9). Multiple COI sequences are available on GenBank for Brown Garden Snails (e.g., Grande *et al.*, 2004; Greve *et al.*, 2010; Neiber *et al.*, 2011; Régnier *et al.*, 2011; Rada *et al.*, 2012), which occur in three distinct genetic groups, with all Australian Brown Garden Snail specimens examined being closely related to each other, matching closely with specimens previously examined from western Europe (Fig. 9). The four Helicidae species examined here, including additional sequences available on GenBank (i.e. previously examined *C. aspersum, C. apertus, E. vermiculata* and *T. pisana*), differ from each other by an average of more than 15% (Table 5, Fig. 9).

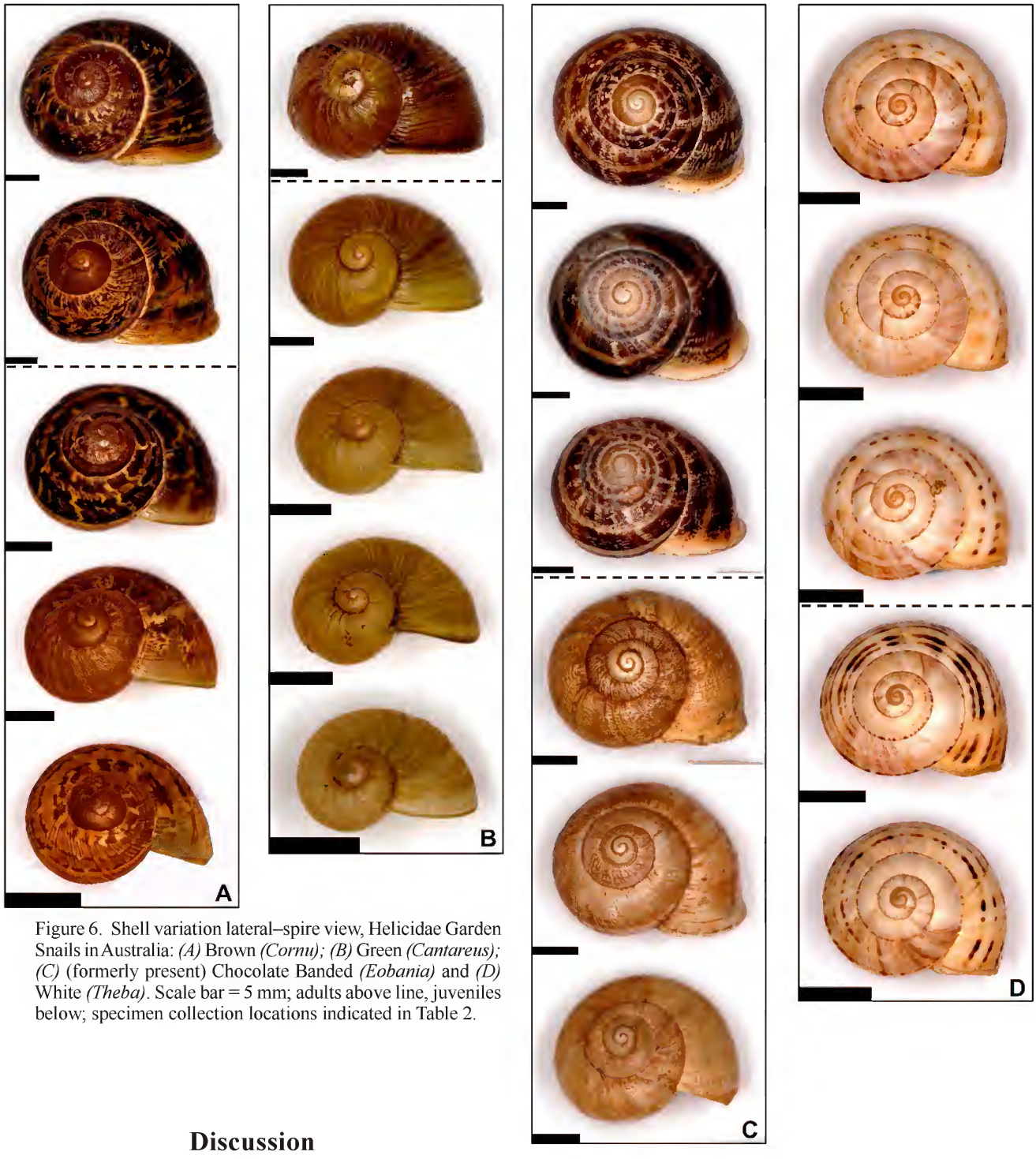

Figure 6. Shell variation lateral–spire view, Helicidae Garden Snails in Australia: *(A)* Brown *(Cornu); (B)* Green *(Cantareus); (C)* (formerly present) Chocolate Banded *(Eobania)* and *(D)* White *(Theba)*. Scale bar = 5 mm; adults above line, juveniles below; specimen collection locations indicated in Table 2.

Discussion

Identification of Helicidae in Australia

Many higher level groups of mollusc are yet to be fully phylogenetically resolved, however the family Helicidae is a well-supported group both morphologically and genetically (Wade *et al.*, 2008; Razkin *et al.*, 2015). Examinations of literature and collection reference specimen records (present study) show that only four species (in four genera) of Helicidae (approximately 1% of the world fauna) appear to have managed to establish in Australia to date—with one of these now locally extinct—despite regular border interceptions of a number of other helicid species (e.g., Table 3).

The four helicid species (above) belong to different genera (however, see Systematics section), and all differ considerably both morphologically and genetically (as demonstrated by the present study). Currently, there are a large number of reference DNA barcode sequences available, with more than 160 Helicidae species (i.e. approximately 40% of species worldwide) already represented on the BOLD database (accessed March 2015). The large genetic differences observed between species make a DNA barcoding approach an extremely valuable tool for confirming the identity of introduced helicid species, as there are a large number of morphologically similar potential

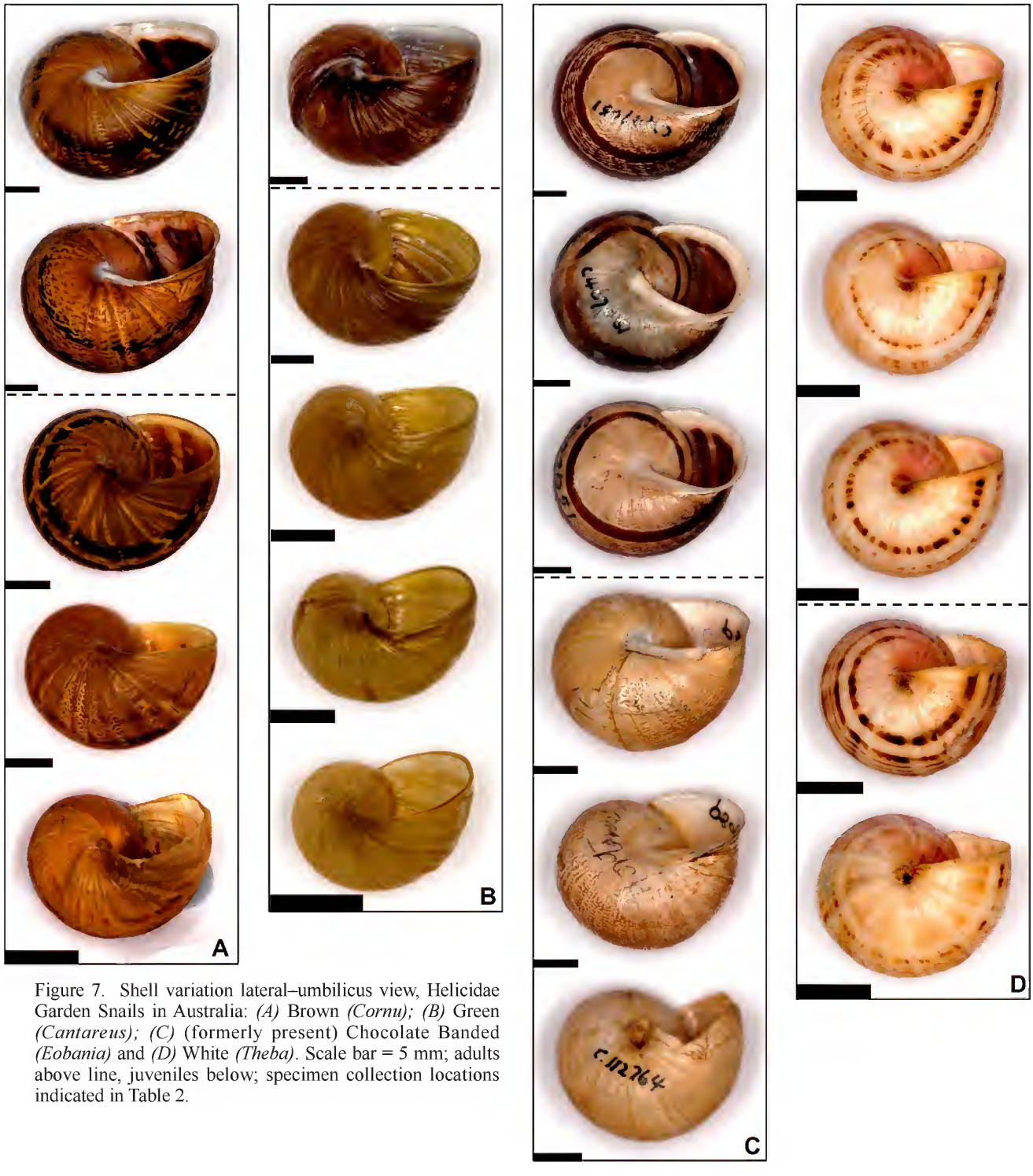

Figure 7. Shell variation lateral–umbilicus view, Helicidae Garden Snails in Australia: *(A)* Brown *(Cornu); (B)* Green *(Cantareus); (C)* (formerly present) Chocolate Banded *(Eobania)* and *(D)* White *(Theba)*. Scale bar = 5 mm; adults above line, juveniles below; specimen collection locations indicated in Table 2.

exotic species of Helicidae worldwide (Schileyko, 2006), some only recently described (e.g., Mumladze *et al.*, 2008), with most morphological keys usually only dealing with specific geographic regions (e.g., Yildirim, 2004; present study). Fortunately, members of additional helicid genera, including those intercepted in recent years—*Arianta, Cepaea, Helix, Marmorana* and *Otala* (L. Watson, pers. comm.)—also appear genetically distinct (Fig. 9).

Genetic variation in Australia

Although sampling was relatively limited in the present study, it does provide an initial indication of potential source populations for Brown and White Garden Snails. Multiple lineages of Brown Garden Snails are known to have spread across the world (Madec *et al.*, 2003; Guiller & Madec, 2010; Galtán-Espitia *et al.*, 2013). In Australia Brown Garden Snails are believed to have been introduced from northern Europe (Smith, 1992), in the present study all Australian *Cornu aspersum* specimens appeared closely related to each other, and were most similar to those previously tested from western Europe (Fig. 9).

Table 3. Recent Australian border interceptions of Helicidae species. (Sourced from OSP Bulletins: June 2011–June 2012, L. Watson pers. comm.).

species	date	state	source	from
Eobania vermiculata	2011-Oct	SA	external container	China
Cantareus apertus	2011-Oct	WA	old Ford utility	USA
Cepaea nemoralis	2011-Dec	Qld	external container	Germany
Eobania vermiculata	2011-Dec	WA	steel formwork	Ireland
Eobania vermiculata	2012-Jan	Qld	external container	Spain
Cepaea nemoralis	2012-Jan	Qld	external container	China
Eobania vermiculata	2012-Mar	SA	container	Unknown
Eobania vermiculata	2012-Jun	Qld	used machinery	Italy
Arianta arbustorum	2012-Jun	Qld	railway wagons	China

Table 4. *(A)* Shell size measurements (ranges, mm) and *(B)* Statistical tests, Discriminant Function Analyses (DA) and Principal Component Analyses (PCA), for four species of Helicidae Garden Snails. Factor 1 accounts for more than 90% of the observed variation. Measurement abbreviations: *AW*, aperture width; *BW*, body-whorl height; *SH*, shell height; *SW*, shell width; and *W*, height of whorls (see Fig. 3).

	SW	AW	SH	BW	AH	W
A						
Brown *(Cornu)*	9.6–31.1	6.0–20.5	8.4–30.6	8.1–27.4	7.1–20.6	0.3–3.2
Green *(Cantareus)*	10.2–25.9	6.7–16.1	9.4–25.1	9.0–23.9	8.3–19.6	0.1–1.6
Chocolate Banded *(Eobania)*	22.1–30.8	12.8–19.4	15.9–24.3	13.8–20.4	11.8–16.7	2.0–4.3
White *(Theba)*	7.7–20.6	4.7–12.9	5.4–15.6	4.8–13.6	4.0–10.8	0.4–2.2
B						
Variable Multicolinearity–Tolerance Statistic (DA)	0.02	0.01	0.01	0.01	0.05	0.00
Correlation between each variable with Factor 1 (DA)	0.5	0.4	0.1	-0.1	-0.1	0.7
Contribution (%) of each variable to Factor 1 (PCA)	18.0	18.5	18.7	17.2	16.5	11.1

Table 5. Average DNA differences (COI locus) within (grey-shaded) and between Helicidae Garden Snail species.

	within sp.	Brown	Green	Chocolate	White
Brown *(Cornu)*	2.6	—	—	—	—
Green *(Cantareus)*	1.5	15.5	—	—	—
Chocolate Banded *(Eobania)*	2.0	16.2	18.4	—	—
White *(Theba)*	5.5	17.6	18.2	18.5	—

White Garden Snails *(Theba pisana)* were first detected in Western Australia in the 1890's (Johnson, 1988), before spreading east, reaching South Australia by 1928 (Pomeroy & Laws, 1967), and the eastern states by the 1990's (Baker, 1986, 2002; Sanderson & Sirgel, 2002). Our study confirms that eastern Australian specimens belong to the subspecies, *Theba pisana pisana*, with the COI haplotype found here being extremely similar genetically (though not identical, see Fig. 9) to a haplotype detected in specimens previously examined from Western Australia, South Africa and the Netherlands (Daumer *et al.,* 2012). Future genetic assessments of additional populations across Australia would be valuable in understanding the introduction history of this species in Australia.

Detailed studies screening population molecular variation in all Helicidae species in Australia would be valuable in assessing the introduction history and possible original source populations of each species. Genetic assessments for the other two species (Green and Chocolate Banded Snails) were not possible in the present study. Australian Green Garden Snails are believed to have been originally introduced from southern Europe (Smith, 1992), however possible source populations of the eastern Australian specimens (either internationally or from within Australia) are yet to be examined. Possible source populations of Chocolate Banded Snails are beginning to be examined worldwide with a number of *Eobania vermiculata* subspecies recognised (e.g., Rada *et al.,* 2012), however, *E. vermiculata* was only available as dry shells in the present study.

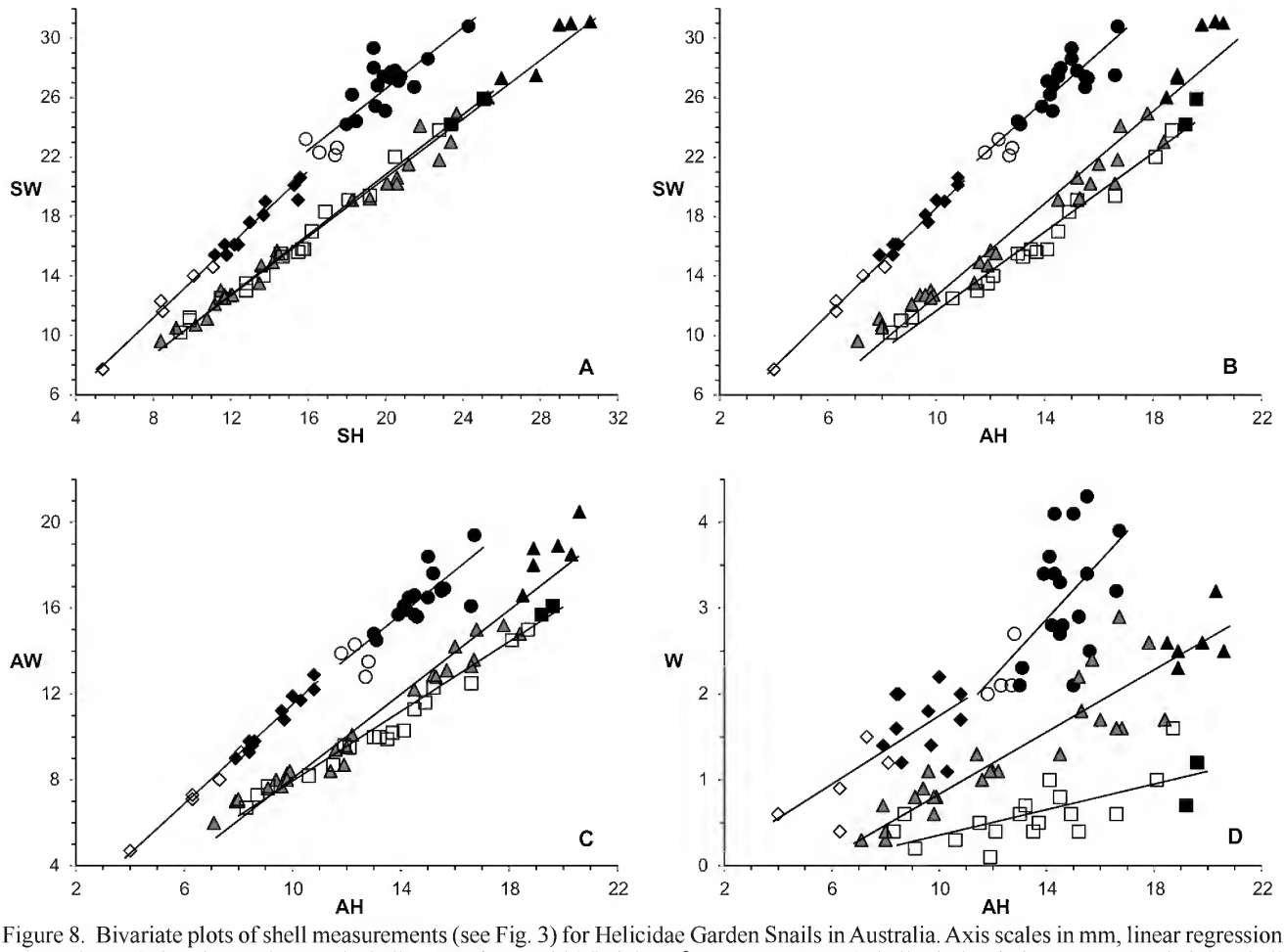

Figure 8. Bivariate plots of shell measurements (see Fig. 3) for Helicidae Garden Snails in Australia. Axis scales in mm, linear regression values shown below in brackets. *(A)* Shell proportions: width/height ($R^2 = 0.73–0.99$); *(B)* shell width relative to aperture height: shell width/aperture height ($R^2 = 0.77–0.99$); *(C)* aperture proportions: width/height ($R^2 = 0.71–0.99$); *(D)* development of whorls: height of whorls/aperture height ($R^2 = 0.36–0.85$). Symbols: ▲ *Cornu;* ■ *Cantareus;* ● *Eobania* and ◆ *Theba*. Adults: black filled shapes; juveniles: unfilled symbols *(Cantareus, Eobania, Theba)* or grey *(Cornu)*.

Green Garden Snails in eastern Australia

Generally, dispersal of garden snails is known to occur both (relatively slowly) naturally from adjacent areas and (relatively quickly) through colonisation to new areas accidentally on human transported goods (e.g., Hely *et al.,* 1982; Barker & Watts, 2002; Peltanová *et al.,* 2012). Human mediated transport is no doubt responsible for Green Garden Snails becoming established in eastern Australia. The first detection occurred on a property near Cobram in north-eastern Victoria in September 2011 (specimens listed in Systematics section). As part of Biosecurity DEDJTR Victoria's surveillance and eradication activity, regular field surveys were conducted until December 2011 on the original property as well as adjoining properties. Currently, there is still restricted movement of plant material and limited surveillance for Green Garden Snails being carried out in Victoria (G. Berg, pers. comm.).

Earlier historical records of Green Garden Snails from Hobart, Tasmania, cited by Kershaw (1991) appear to be an error, as the original record in Petterd & Hedley (1909) refers to *Geostilbia aperta* (Swainson) which is not a member of Helicidae (family Ferussaciidae), rather than *Helix aperta* (synonym for Green Garden Snails). The ferrussaciid referred to in Petterd & Hedley (1909) was probably *Cecilioides acicula*, a species which still occurs near Hobart (M. Shea, pers. obs.).

Conclusions

Introduced Helicidae garden snails in Australia are associated with human modified habitats and can be serious pests, being generalist feeders and capable of breeding up to large numbers. Our study has shown that a relatively small number of species (n = 3) are currently established in Australia, however future incursions of other exotic helicids are very likely. We provide a baseline which should assist in the early detection of any additional newly introduced Helicidae species into Australia. We have also documented the first occurrence of Green Garden Snails in eastern Australia where they may become a significant agricultural pest. Accurate species identification of all lifestages is essential for biosecurity (e.g., Blacket *et al.,* 2012, 2015) and in the present study introduced Helicidae snail adults were found to be morphologically distinctive for a number of diagnostic size, colour and pattern differences in shell and body morphology, however the juveniles can be problematic. The large degree of molecular differentiation observed between these species could be used to identify suspect-exotic specimens in a DNA barcoding approach, and should prove especially valuable for identification of small juvenile specimens.

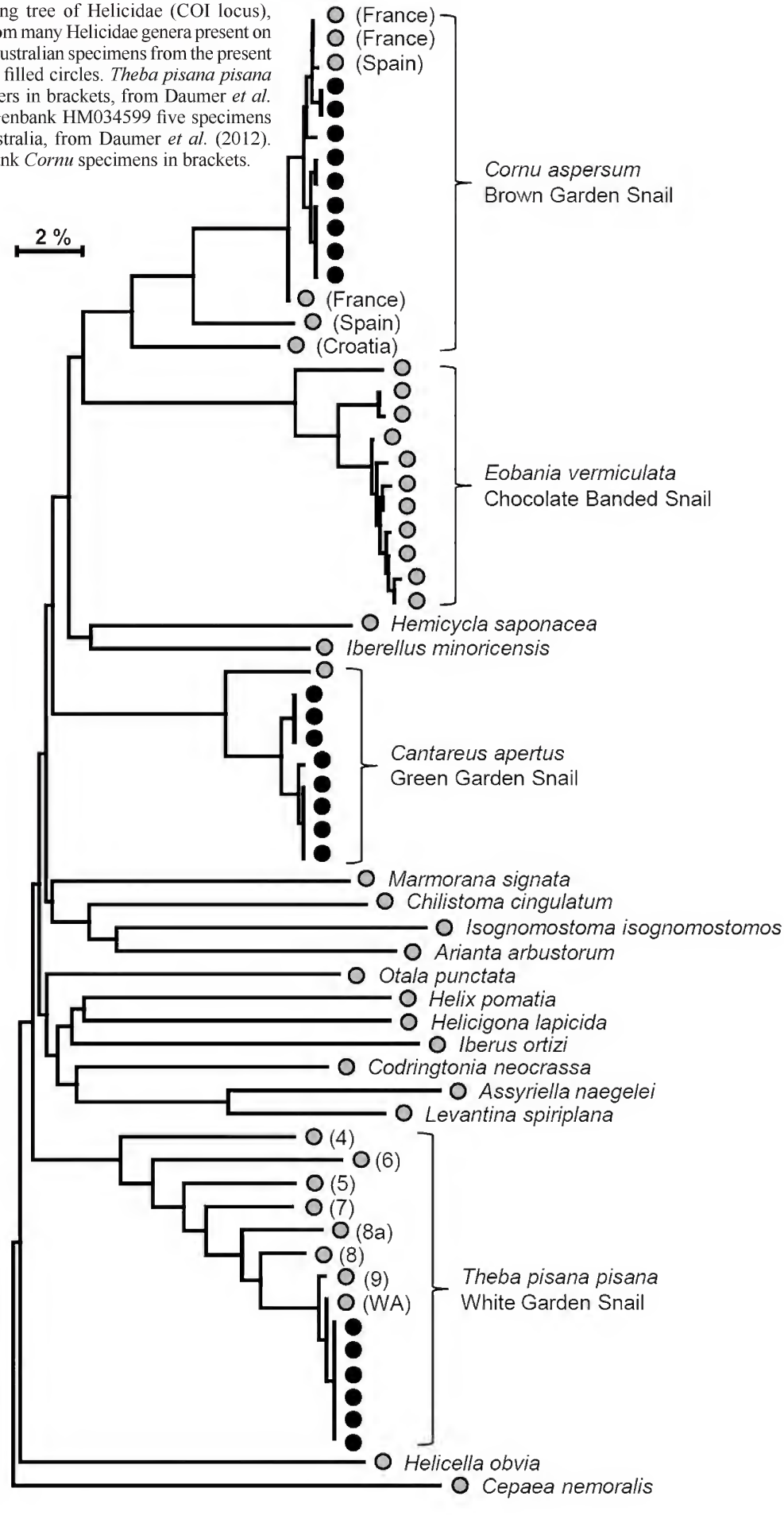

Figure 9. Neighbour-joining tree of Helicidae (COI locus), including DNA sequences from many Helicidae genera present on GenBank. Sequences from Australian specimens from the present study are indicated as black filled circles. *Theba pisana pisana* lineages indicated by numbers in brackets, from Daumer *et al.* (2012), *T. pisana* (WA) = Genbank HM034599 five specimens collected from Western Australia, from Daumer *et al.* (2012). Country of origin for Genbank *Cornu* specimens in brackets.

Systematics

GASTROPODA

STYLOMMATOPHORA

Family HELICIDAE Rafinesque, 1815

Genus *Cornu* Born, 1788

Cornu aspersum (Müller, 1774)

Objective synonyms—*Helix aspersa, Cantareus aspersa, Cryptomphalus aspersus.*

Common names—Brown Garden Snail, Common Garden Snail.

Material examined. *New South Wales:* AM C121130 Jenolan Caves; AM C430603 St. Peters, Sydney; AM C430605 Seal Rocks headland south of Forster; AM C430607 Timor Caves camping ground, Upper Hunter River; AM C456977 east of Glen Davis at end of Capertee River track; AM C430602 Swansea, south of Newcastle. *Victoria:* Blackburn South VAITC3037, VAIC ×1; Cobram VAITC3072, 3073; Doncaster VAITC3022, VAIC ×3; Knoxfield VAITC3015, 3071, VAIC ×7; Irymple VAITC3077, 3078, 3080, VAIC ×11; Preston VAITC3076, VAIC ×4; Ringwood East VAITC3047, 3048, VAIC ×5.

Diagnosis. Shell: large (up to 4 cm), thin, raised spire, globose, 4–5 whorls increasing rapidly with body-whorl greatly flared, aperture large and rounded, umbilicus closed, shell lip thickened white and strongly reflected out in adults, rounded whorls in both adults and juveniles. Shell colour: light brown with darker spiral bands and yellow flecks. During aestivation: possesses either thin and clear or thickened and greyish green epiphragm, that is not convex positioned inside the aperture. Soft body: greenish-grey with a pale dorsal stripe. Adults: identified by the presence of a thickened reflected lip, indicating maturity and the cessation of growth (*sensu* Madec *et al.,* 2003).

Distribution in Australia. Present in parts of all Australian states and territories.

Remarks. The species identification of VAITC specimens (above) was confirmed in the present study through DNA barcoding (ITS2 & COI) and comparison with validated AM specimens. In this study we employed the generic name *Cornu,* as is currently accepted (ICZN Case 3518—ICZN, 2015). Phylogenetic estimates of relationships within Helicidae show that Green and Brown Garden snails are closely related based on both 16S (Manganelli *et al.,* 2005; Groenenberg *et al.,* 2011; Razkin *et al*., 2015) and ITS2 (Wade *et al.,* 2006; Régnier *et al.,* 2011; Razkin *et al*., 2015) DNA sequences, with most of these previous studies placing these two species in the same genus, *Cantareus,* as proposed by Guisti *et al.* (1996), on the basis of a shared morphological internal synapomorphy. However, the majority of recent studies place Brown Garden Snails in *Cornu* (as in the present study). Indeed, in the present study Brown and Green Garden Snails do appear to be substantially genetically distinct based on COI variation (Table 5, Fig. 9), adding some support to the placement of these species in different genera. The placement of Brown Garden Snails in the genus *Helix* is not supported by molecular evidence, with species of *Helix* now placed in a different tribe from *C. aspersum* and *C. apertus* (e.g., Razkin *et al*., 2015). *Cornu* currently contains a single species (CABI species datasheet, http://www.cabi.org/isc/datasheet/26821).

Genus *Cantareus* Risso, 1826

Cantareus apertus (Born, 1778)

Objective synonym—*Helix aperta.*

Common names—Green Garden Snail, Green Snail, Singing Snail.

Material examined. *Victoria:* Cobram VAITC3032–3036, 3103, 3104, VAIC ×10; Cobram South VAITC3014, 3018, 3019, 3020, 3021, 3066–3070, VAIC ×9. *Western Australia:* AM C135546 Wanneroo, north of Perth; VAIC Neerabup ×2.

Diagnosis. Shell: medium (up to 3 cm), very thin, low spire, globose, 3–4 whorls increasing rapidly with body-whorl greatly flared, aperture extremely large and rounded, umbilicus closed, shell lip thickened white internally only and not reflected out in adults, rounded whorls in both adults and juveniles. Shell colour: olive green to brown with no banding pattern. During aestivation: possesses convex white thick epiphragm, extending from edge of aperture. Live animal: can make a distinctive noise when disturbed. Soft body: usually cream to dark-grey coloured, with dark dorsal stripes. Adults: identified by size and degree of thickening of the shell-lip.

Distribution in Australia. Present in WA at Wanneroo, Neerabup NP, Herne Hill and Bayswater, Perth; and in north-eastern Victoria, near Cobram.

Remarks. The species identification of VAITC specimens (above) was confirmed in the present study through DNA barcoding (ITS2 & COI) and comparison with validated AM specimens. Formerly regarded as belonging to *Helix*, it is now considered to be in the genus *Cantareus* (Schileyko, 2006), see ICZN comments above under *Cornu*. *Cantareus* currently contains a single species (Schileyko, 2006).

Genus *Eobania* Hesse, 1913

Eobania vermiculata (Müller, 1774)

Objective synonym—*Helix vermiculata.*

Common names—Chocolate Banded Snail, Chocolate-band Snail.

Material examined. New South Wales: Sydney, Bronte, Waverley Cemetery AM C407051 ×18 (adults); Sydney, Ryde AM C089089 ×4 (juveniles); Sydney, Ryde AM C112764 ×4 (juveniles with damaged lips).

Diagnosis. Shell: medium (up to 3 cm), thick to thin, short and wide, raised spire, subglobose, 5 whorls, body-whorl moderately flared, aperture small and compressed, umbilicus closed, shell lip thickened white and strongly reflected out in adults, rounded whorls in both adults and juveniles. Shell colour: light brown to yellow usually with continuous thick dark brown and white spiral bands and yellow flecks. Soft body: cream with a dark mantle (Stanisic *et al*., 2010). Adults: identified by strongly reflected lip and a well-developed columellar plait covering the umbilicus (Stanisic *et al*., 2010).

Distribution in Australia. Locally extinct, formerly present in NSW, near Sydney, and Leven River, Ulverstone Tasmania, but no longer occurs at either location.

Remarks. Validated AM specimens were used for species identification in the present study. *Eobania* currently contains a single species (Schileyko, 2006), with several subspecies present in the natural range of *E. vermiculata* (e.g., Rada *et al.,* 2012). The sub-specific designation of the Australian specimens is not yet determined.

Genus *Theba* Risso, 1826

Theba pisana (Müller, 1774)

Objective synonym—*Helix pisana.*
Common names—White Garden Snail, White Gardensnail, White Italian Snail.

Material examined. *New South Wales:* AM C088901 Nelson Bay, Port Stephens; AM C206180 Redhead Beach, Newcastle; AM C168582 Avalon Beach, Sydney; AM C407047 Waniora Point, Bulli; AM C348456 Cunjurong Point, E of Lake Conjola; AM C404152 Cudmirrah Beach near Sussex Inlet; AM C334544 Aslings Beach, Twofold Bay, Eden. *Victoria:* Venus Bay VAITC3831–3837, VAIC ×10; Port Campbell VAIC ×3, 3 km North Port Campbell VAIC ×3.

Diagnosis. Shell: small (up to 2 cm), thick to thin, tall and narrow, raised spire, subglobose, 5 whorls, body-whorl moderately flared, aperture medium and rounded, narrow umbilicus, shell lip thickened pink internally only and not reflected out in adults, whorls rounded in adults angulate in juveniles. Shell colour: white usually with broken thin dark brown spiral bands and chevrons. Soft body: pale overall. Adults: identified by the presence of rounded body-whorls (Stanisic *et al.,* 2010).

Distribution in Australia. Present in southern Australia: NSW, Tas., Vic., SA, WA.

Remarks. The species identification of VAITC specimens (above) was confirmed in the present study through DNA barcoding (ITS2 and COI) and comparison with validated AM specimens. The genus *Theba* contains at least 18 species in its natural range (Greve *et al.,* 2010), but only *Theba pisana pisana* occurs worldwide (e.g., Cowie *et al.,* 2009; Greve *et al.,* 2010; Däumer *et al.,* 2012). Australian specimens belong to *T. p. pisana* (Däumer *et al.,* 2012; current study). CABI species datasheet: http://www.cabi.org/isc/datasheet/62094.

AUTHOR CONTRIBUTION STATEMENT. All authors were involved in the conception and design of this research, identifying diagnostic specimens during the initial eastern Australian detection of Green Garden Snails, and contributing to the systematics section. MB conducted the morphometric and molecular experimental work, and produced the specimen images (apart from Figs 2 and 4). MS provided expert support through validating identifications of reference specimens, providing unpublished background information and assisting with the morphometrics section. All authors collected snails for this study and contributed to the writing of the manuscript.

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